Energy Research and Development Division
FINAL PROJECT REPORT

Habitat Modeling, Landscape Genetics, and Habitat Connectivity for the Mohave Ground Squirrel to Guide Renewable Energy Development

USGS
science for a changing world

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PREFACE

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Habitat Modeling, Landscape Genetics and Habitat Connectivity for the Mohave Ground Squirrel to Guide Renewable Energy Development is the final report for the Potential Habitat Modeling, Landscape Genetics and Habitat Connectivity for the Mohave Ground Squirrel project (contract number 500-10-027) conducted by the United States Geological Survey. The information from this project contributes to Energy Research and Development Division's Energy-Related Environmental Research Program.

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ABSTRACT

Mohave ground squirrels inhabit a restricted range in the northwest Mojave Desert in California and are protected as a California Threatened species because of anthropogenic habitat loss. Proposed wind and solar energy development threaten to further reduce habitat. This research had four sequential integrated components: 1) habitat suitability models were used to describe current habitat and to evaluate losses from anthropogenic development and proposed energy development; 2) derivations of downscaled climate data from two emissions scenarios were incorporated to project future habitat, which were evaluated with respect to different time periods (2030 and 2080) and proposed energy development; 3) a simulation approach was used to examine how habitat shifts due to climate change would impact genetic diversity patterns; and 4) critical connectivity areas were determined using habitat models in conjunction with current land use and renewable energy development scenarios using least-cost and graph theoretic analyses. The initial habitat suitability model predicted suitable habitat covering 19,023 square kilometer prior to European settlement. Impact scenarios predicted that between 1,884 square kilometers and 3,096 square kilometers of suitable habitat have been lost to human disturbances and an additional 10 percent may be affected by renewable energy development in the near future. Climate change may reduce current habitat area up to 57 percent by 2030 and up to 84 percent by 2080. There were three genetic groups found in the northern, central, and southern portions of the range. The results highlighted geographic areas that may serve as important pathways for facilitating gene flow among populations and allowing movement in response to climate change. Based on these analyses, some populations may experience dramatic declines in site occupancy and genetic diversity. Data from this project was being used to develop conservation and energy alternatives for the Desert Renewable Energy Conservation Plan and to assess impacts.

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EXECUTIVE SUMMARY

Introduction

Global recognition of climate change coupled with energy independence goals has focused national attention on renewable energy. The abundance of potential solar and wind energy and expansive public lands make the southwestern United States a primary candidate for utility-scale renewable energy development. Renewable energy has many beneficial results but it competes for space with other public land uses. Natural resource stewards face the difficult task of balancing diverse land use needs and sensitive species such as the Mohave ground squirrel (*Xerospermophilus mohavensis* Merriam) require additional consideration. The Mohave ground squirrel only resides in portions of the Mojave Desert in southern California. Its distribution is among the smallest for North American squirrels. Habitat modification resulting from urban development, utility infrastructure, transportation corridors, military training, and recreational activities has raised concern for the future survival of this species. The Mohave ground squirrel is protected as a Threatened species under the California Endangered Species Act. It was petitioned for listing under the federal Endangered Species Act in 2005, but the United States Fish and Wildlife Service found that federal listing was not warranted at that time. More recent initiatives to stimulate economic growth by developing renewable energy using solar, wind, and thermal power sources may disturb additional habitat; however the potential effects on the squirrel have not been evaluated comprehensively. Lack of detailed distribution and habitat information for the Mohave ground squirrel has been identified as a barrier to permitting of renewable energy development projects.

Project Purpose

The goal of this project was to advance the knowledge of Mohave ground squirrel habitat, distribution and genetics in relation to climate change and renewable energy to provide rigorous, scientifically-based information to use in regional planning efforts, with the potential to identify areas where renewable energy could be developed with minimal impact to the squirrel. This research effort consisted of four sequential integrated components:

1) Habitat suitability models for the Mohave ground squirrel were developed to describe current habitat and to evaluate losses due to anthropogenic development and proposed energy development.
2) Derivations of climate data from two emissions scenarios were incorporated in the habitat suitability model to predict future habitat in two time steps (2030 and 2080). Habitat shifts due to climate change were evaluated with respect to different time periods and proposed energy development.
3) A simulation approach was used to examine how habitat shifts due to climate change may impact patterns of genetic diversity.
4) Critical connectivity areas were determined using habitat models in conjunction with current land use and renewable energy development scenarios.

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Project Results

A map of habitat suitability for the Mohave ground squirrel was developed and impacts from historic land use and planned renewable energy development were identified. Data on all known locations of squirrels were assembled from many sources including scientific literature, agency databases, Mohave ground squirrel experts, and contributions from ongoing research projects. Researchers identified factors that limit or support populations of Mohave ground squirrel such as rainfall, temperature, and soil that could be used to build a predictive habitat model. Eighty-six different combinations of environmental factors were analyzed to identify the best factors for predicting habitat. The best model included: 1) an estimate of the surface texture of the land, which ranged from sandy playas to rocky slopes; 2) the light reflectance of the land surface representing different land forms; 3) a measure of soil water stress as an indicator of the potential for supportive vegetation while considering the underlying soils; and 4) cumulative winter precipitation that provide water for squirrels as well as vegetation.

The habitat suitability model estimated that Mohave ground squirrel habitat encompassed 19,023 square kilometers (km^2) prior to European settlement of the desert. Sixteen percent of pre-European habitat has already been impacted or lost to human land uses such as urbanization and agriculture. An additional ten percent of habitat may be affected by renewable energy development on public lands in the near future based on Bureau of Land Management Solar Energy Zones, designated transmission corridors, and permit applications for renewable energy projects. Mohave ground squirrel habitat suitability was estimated to be higher in areas slated for renewable energy development than surrounding areas. Proposed development of wind energy posed the greatest threat to habitat, with 503 km^2 to 522 km^2 of suitable habitat in areas of proposed development and only two km^2 of suitable habitat in areas proposed for solar energy development.

The influence of climate change on the potential distribution of Mohave ground squirrel habitat was estimated and the effect of renewable energy on future distributions was determined. There was general agreement that climate change will result in hotter, drier conditions in the American southwest. Two scenarios of future greenhouse gas emissions were used to forecast potential climate change through time, representing the broadest range of expected climate change. These scenarios were developed by the Intergovernmental Panel on Climate Change and were designated A2-high and B1-low. Future suitable habitat was predicted for two time periods, 2030 and 2080. Predictions of future habitat were compared to estimates of current habitat using the habitat suitability model, including consideration of proposed utility-scale renewable energy development.

Under future climate forecasts some habitat becomes unsuitable, while new areas may open up as suitable habitat. By 2030, 57 percent and 52 percent of current habitat may be lost in the A2 and B1 emissions scenarios, respectively. By 2080, roughly 84 percent of current habitat was predicted to be lost under either of the emissions scenarios. Predictions of suitable habitat for the A2 and B1 emissions scenarios added 7,876 km^2 and 8,151 km^2 of new habitat, respectively. However, by 2080 total predicted habitat decreased substantially (below current and 2030 totals), including losses of new (2030) habitat.

Habitat predictions under future climate scenarios indicated that the majority of habitat for the Mohave ground squirrel will likely be located in the Owens Valley north of Ridgecrest up to Bishop, California. Areas considered habitat under both of the emissions scenarios that overlapped with proposed wind projects were found west and south of Ridgecrest, CA in 2030 and 2080. Some areas of new habitat resulting from climate change were not within the current predicted distribution and may be unreachable by individuals due to natural and man-made barriers to movement without human intervention such as through assisted migration. In the context of renewable energy there were additional predicted losses (above those attributed to climate change) of 615 km^2 (three percent) and 641 km^2 (four percent) of current habitat by 2030 for the A2 and B1 emissions scenarios, respectively. By 2080, an additional 290 km^2 (two percent) and 222 km^2 (1.5 percent) were predicted to be lost to renewable energy if development proceeds according to current proposals.

Understanding Mohave ground squirrel genetic variation was central to establishing land use practices that may sustain the species. Mohave ground squirrel genetic structure was analyzed from broad geographic and temporal scales, and then narrowed to regional patterns of variation within the species, ending with a fine-scale view within a particularly well-sampled population. Genetic information was linked to the habitat suitability model and landscape connectivity data by examining whether patterns of genetic dissimilarity were correlated with habitat-based distances among localities. Finally, a simulation approach was used to begin examining how various climate change scenarios might impact patterns of genetic diversity in this species.

Current patterns of genetic variation within the Mohave ground squirrel were the result of both historic and ongoing processes. The species was characterized by three genetic groups found in the northern, central, and southern portions of the range, respectively. The deepest genetic subdivision within the species coincided spatially with the Owens River system, and this probable historic barrier to gene flow still explained the greatest portion of genetic subdivision within the species. Nonetheless, localities that were connected by multiple potential routes of suitable habitat experienced more genetic exchange over time. The Freeman Gulch area was characterized by suitable habitat and long-term occupation and within this area the spatial scale of genetic structure suggested dispersal distances in this species of approximately one kilometer, consistent with previous direct estimates. Available models predicted dramatic declines in site occupancy and genetic diversity in and around the Freeman Gulch area using a process modeling approach that explored the potential impact of climate change on Mohave ground squirrel populations. Significant gaps in knowledge at all spatial scales of investigation and areas of particularly high research need were highlighted. The consequences of habitat change related to renewable energy development may be accentuated in light of predicted genetic loss related to climate change.

The research team built on the previously described research to develop a comprehensive spatial analysis of Mohave ground squirrel landscape connectivity across the entire range of the species under current conditions and future scenarios representing climate change and energy development. Estimates of potential habitat provided a useful starting point for defining critical areas for Mohave ground squirrel conservation, but did not address the relative importance of habitat patches for facilitating their movement through the landscape. Landscape connectivity

analysis quantified the importance of habitat for Mohave ground squirrel dispersal and movement processes. Large habitat patches that provided adequate habitat to support Mohave ground squirrel populations may be less subject to local extinctions and may serve as a source of emigrants to replenish other areas that have lost their populations. If a large habitat patch was isolated, its connectivity role would be limited compared to a patch that was centrally located and well connected. Furthermore, some habitat areas that did not support large populations may provide important connections among critical source populations. These "stepping-stone" areas often had a disproportionately large role in supporting overall habitat network connectivity and should be considered for conservation prioritization due to their value for facilitating movement that may exceed their habitat value. This analysis also informed the landscape genetics analysis by developing maps of resistance to movement that were subsequently compared to genetic distance.

At least 14 areas were deemed "important connectivity areas" linking some isolated habitat clusters with larger core areas. Important connectivity areas were located throughout the Mohave ground squirrel range and included locations such as Fremont Valley, Cuddleback Lake, the areas south, east, and west of Ridgecrest, Coso Basin, and Cactus Flat. The site with the highest connectivity value was located within Edwards Air Force Base adjacent to Rogers Dry Lake. The Coso Basin is exceptionally important because that area is the current "gateway" to the northern populations. Mohave ground squirrel habitat was well connected, suggesting that movement was likely between the core habitat areas. However, habitat lost through land-use development was disproportionately important to Mohave ground squirrel connectivity compared to the effects of roads, agriculture and other land-use types. Potential impacts of climate change appeared to exceed past and current human impacts with respect to both Mohave ground squirrel habitat and overall landscape connectivity, and resulted in dramatic fragmentation of currently suitable habitat areas. The most likely route of Mohave ground squirrel movement in response to climate change was restricted to the west side of Owens Lake and up the east side of Owens Valley. Pinch points where movement was funneled because of restricted habitat suitability were important because they represented areas of high conservation priority given the assumptions of habitat models, landscape connectivity models, and climate change forecasts. A pinch point existed along the west side of Owens Lake where steep mountain slopes approach Highway 395. Movement corridors that connected the central and northern regions differed depending upon the climate scenario that was used for estimating resistance to movement.

Renewable energy development including solar, wind, and transmission corridors decreased habitat by 2.8 percent assuming current climate, 3.6 percent in 2030 using the A2 scenario, and 4.6 percent in 2080 using the A2 scenario. Although the overall loss of habitat was relatively small, much of the lost habitat lies within important core areas and will likely have a large effect on genetics. Locally some important links may be severed by these developments given the major changes in future distribution of suitable habitat predicted to result from climate change processes. Loss of even a small number of links might have important consequences for long-term population viability.

The initial habitat suitability model predicted suitable habitat covering 19,023 km²prior to European settlement. Impact scenarios predicted that between 10 percent and 16 percent of suitable habitat has been lost to historical human disturbances, and an additional 10 percent may be affected by renewable energy development in the near future. Changes in climate may reduce current habitat area as much as 57 percent by 2030 and up to 84 percent by 2080. There were three genetic groups found in the northern, central, and southern portions of the range, respectively. The results highlighted areas that may serve as important pathways facilitating gene flow among populations and allowing movement in response to climate change. Based on these analyses, some populations may experience dramatic declines in site occupancy and genetic diversity. Landscape connectivity was critical for maintaining viable populations, maintaining gene flow, and allowing for movement in response to a changing climate. The maps generated in this study can be used for developing sampling designs, evaluating conservation corridors, and informing development planning in the region to minimize and avoid impacts of renewable energy development.

Mohave ground squirrel habitat losses appear imminent relative to climate change, general expansion of human activities, and energy development in particular. The potential losses hypothesized by modeling habitat, its response to climate change, landscape genetics and habitat connectivity were likely an underrepresentation of future conditions because development models only included estimates of renewable energy growth on public lands. State and private lands in the region also have proposals for renewable energy on 260 km², and an additional 3,500 km² may be available for renewable energy. Taking this into account, renewable energy development may impact nearly as much habitat as has been disturbed by previous human expansion into this region, equating a loss of up to a quarter of suitable habitat from pre-European settlement levels within the last century. The analyses conducted here considered the footprint of renewable energy and associated transmission corridors. There are additional indirect sources of disturbance that may be important to Mohave ground squirrels, including: the release of chemicals such as dust suppressants, insulating fluids and herbicides throughout the operational life of facilities; auditory interference from the sound of turbines; increases in predators and invasive species that further alter habitat; and changes in surface flow of water that influence important vegetation in these habitats.

It is important to conserve core areas of high-quality habitat as well as the pathways for individual dispersal and gene flow that provide critical connections among the high-quality habitat areas. These results highlighted the importance of conserving landscape connectivity through north-south trending, low-elevation valleys. Such valleys can function as important corridors for many desert species in facilitating latitudinal migration in response to climate change. Low-elevation valleys were expected to be of particular importance to burrowing rodents such as Mohave ground squirrels for which soil texture is a critical component of habitat. Currently unoccupied habitat may become suitable to the Mohave ground squirrel, but the species' use of these areas assumed that they moved into those areas successfully. Although habitat shifts of this magnitude have occurred in paleohistory, the success of such shifts will also depend on the squirrels' ability to migrate through human-modified landscapes.

The energy development scenario the authors modeled was not a particularly extreme case, given that it was limited to projects already permitted for development. Although implementation of this scenario would only reduce most measures of landscape connectivity by two percent or less, local impacts could be severe and the reduction of habitat quality in areas of core habitat could be expected to negatively affect Mohave ground squirrel populations. In addition, the importance of the developed area to landscape connectivity was predicted to increase by at least three-fold given the climate change scenarios considered. It was thus critically important to consider future land-use and climate change when evaluating the outcome of any planned development for the requirements of biodiversity.

Project Benefits

This project benefitted ratepayers by promoting the state's renewable energy goals and clean energy jobs, while helping to protect the state's fragile desert ecosystems. This project addressed critical data gaps that hinder biological impact assessment and mitigation and have led to costly delays in environmental permitting. Results from this research project will be useful to agencies, researchers, and developers in siting and conservation planning, impact analyses, and mitigation, resulting in fewer environmental impacts. Data on Mohave ground squirrel habitat suitability from this project has been used to develop conservation and energy alternatives for the Desert Renewable Energy Conservation Plan and to assess impacts.

CHAPTER 1:
Introduction

1.1 Background

The Mohave ground squirrel (*Xerospermophilus mohavensis*), named just over a century ago (Merriam 1889), is precinctive to the western Mojave Desert in California, USA, and occupies portions of Kern, Los Angeles, Inyo and San Bernardino counties (Best 1995). Early estimates of the geographic range of the squirrel are just 20,000 km^2 in area (Hall 1981, Zeiner *et al.* 1988-1990), one of the smallest distributions among North American ground squirrel species (Hoyt 1972, P. Leitner – *pers. obs.*). The closest living relative of the Mohave ground squirrel (MGS) is the round-tailed ground squirrel (*Xerospermophilus tereticaudus*). Mohave ground squirrels have a "shorter tail with distichous hairs and white undersurface", but visual differences between the two species are subtle (Hafner and Yates 1983). Speciation likely occurred when portions of the parent population were isolated 4-1.6 million years ago during the accelerated uplift of the Sierra Nevada, the Transverse Ranges and the Mojave River system, resulting in separation and isolation with MGS evolving in refugia (Hafner 1992, Bell et al. 2009). Subsequently, fluvial-lacustrine systems in the Mojave River basin provided vicariance features during the Pleistocene (Hafner 1992, Bell et al. 2009). Responding to previous climate change, the two species potentially migrated into their current ranges from southern refugia after the Last Glacial Maximum, eventually abutting each other along the Mojave River (Hafner and Yates 1983). The species are capable of hybridizing, but intercrosses appear to be rare, and sampling near the zones of potential hybridization remains limited (Bell and Matocq 2011). The only other similar sized squirrel occupying the range of MGS is the white-tailed antelope ground squirrel (*Ammospermophilus leucurus*) whose range entirely overlaps MGS, but is easily distinguished by its bright white dorso-lateral stripes (Best 1995).

Mohave ground squirrels occupy a harsh desert environment with surface temperatures ranging from around 0 °C to over 50 °C and periods of many months with zero precipitation (Turner 1994). Adult individuals are primarily active during a brief period from February to the end of July (Best 1995). Mohave ground squirrels are adapted to warm temperatures and may go into torpor at temperatures below 27 °C (i.e., about room temperature, Bartholomew and Hudson 1961). They occupy a variety of mixed shrub communities in the region and have also been sighted in alfalfa (*Medicago* spp.) fields. The foliage of some shrubs in the family Chenopodiaceae are important food plants for MGS, including winter fat (*Krascheninnikovia lanata*) and spiny hop sage (*Grayia spinosa*), especially during drought (Bell et al. 2009). Interestingly, both plant species have distributions extending much further north and east than the distribution of the squirrels (Benson and Darrow 1981). Other important diet items include a variety of herbaceous species, many shrubs, fungi and the seeds of shrubs, cactus and Joshua trees (*Yucca brevifolia*) (Best 1995). Insects are also observed widely in diets (Best 1995). Some water is acquired from plant material, and plant water content may influence diets (Recht 1977). Consecutive years of low production may result in local extirpations (Best 1995).

1.2 Issue statement

Habitat loss has been a major conservation concern in relation to the MGS for decades (Gustafson 1993, Leitner 2008, Bell et al. 2009). Extinction risk is increased by having a small range at the margin of the rapidly expanding Los Angeles metropolitan area, in a region highly sought after for a variety of human activities (Best 1995, Hafner 1998). Land status across the arid southwestern United States has changed dramatically in the past 100 years. Just over a century ago, explorations were completed for the region (e.g., Merriam 1893) and extractive industries (i.e., livestock, and mineral exploration) dominated land use until the 1940's (Case and Alward 1997). Livestock use of the open desert was ubiquitous, reducing plant production and increasing soil compaction, which increased erosion and rainfall runoff (Webb and Stielstra 1979, Fleischner 1994). Land use/status changes occurred rapidly due to the post World War II re-distribution of human populations and the changes in lifestyle brought about by large scale housing developments and advances in cooling systems for households, workplaces, and vehicles that made previously inhospitable sites suitable for occupation by large human populations on a year-round basis (Cooper 1998). This phenomenon would not have been possible without inexpensive energy and infrastructure to power these systems beginning in the early 1930's, and massive water re-distribution projects (citations in Jackson and Kuhlken 2006). The connectivity of the national transportation system increased the availability of goods and services since the 1950s. Perceptions of the Great American Deserts evolved from one of a vast wasteland to a lucrative mecca. Year-round production of agricultural food products was made possible by the large scale re-distribution of water across arid lands from sources such as the Colorado River. After WWII, people immigrated to the area in such great numbers as to sustain full time economies that developed into sprawling urban metropolitan areas (Grimm et al. 2008).

The influence of the human footprint is less concentrated in parts of the Mojave Desert than observed in other portions of the West (Leu et al. 2008). However, recent increases in the cost of fossil fuels and concern for energy security have created new resource challenges, with greater emphasis of energy generation using solar, wind, and geothermal technologies. Infrastructure in support of energy alternatives requires the additional structural footprint of utility corridors across the landscape. These impacts from expanded energy development on MGS must be considered in the advance of siting and permitting renewable energy projects.

Economic and demographic changes resulted in shifts in the spatial relationship of land use/status. Fifty years ago, urbanized areas were insular and imbedded in vast expanses of open area. More recently a shift has occurred and the urbanized areas have filled in (or plan to) large portions of formerly open spaces such that the open spaces are now insular having been dissected and isolated by military training, urbanization, recreational activities, and utility and transportation corridors. This change in the spatial juxtaposition of urban versus open areas creates additional challenges for development and conservation planning.

In recent years the national demand for renewable energy has been supported by public policy initiatives at both federal and state levels (e.g., the American Recovery and Reinvestment Act of 2009 and CA Executive Order S-14-08 and CA Senate Bill X1-2) by encouraging and mandating

the development of renewable energy from multiple sources. Although 1/3 of the area under consideration for energy development occurs on private lands, the predominance of public land in California's Mojave Desert provides further incentives for land development planning within the range of the MGS. Renewable energy projects can require substantial areas of land for implementation. Utility scale solar energy development, as currently implemented, requires large contiguous areas, whereas wind development may be more permeable to squirrels with habitat left in a matrix between wind unit footprints. However, a review of acoustical interference (e.g., wind turbine prop noise) in wildlife identified negative population effects across a wide range of vertebrate species (Chan & Blumstein 2011). Although there are no empirical data to suggest the MGS will be negatively influenced by the indirect effects of renewable energy development, habitat loss and degradation within the footprints of such developments is obvious. However, the extent to which the pattern of development on the landscape is likely to influence MGS populations is largely unknown, and is the focus of ongoing research.

Based on concern about historical changes in the ecoregion, the MGS was protected as a 'rare' species in 1971 and raised to a threatened species under the California Endangered Species Act in 1984 (Gustafson 1993, California Department of Fish and Game 2011). The Act protects the species and its habitat from incidental take from development and other actions. MGS are among the seven species of ground squirrels in North America that are considered at conservation risk (Van Horne 2007), ranked as vulnerable to extinction on the International Union for the Conservation of Nature red list of threatened species (IUCN 2012), and imperiled or vulnerable with a moderate to high risk of extinction on the Global Conservation Status Rank list (NatureServe 2004).

As with any species, how the MGS will respond to climate change is unknown, yet this topic is of primary concern because future climate predictions for the region include hotter and drier conditions, and this species already inhabits such environmentally challenging habitats. The influence of climate on species distributions has been studied extensively, with many clear relationships between regional climates and the distribution and diversity of species (Pianka 1966, Woodward 1987, Campbell *et al*. 2009). However, the consequences of a changing climate are still a topic of much research, with some studies suggesting that the distributions of many North American flora and fauna species will be reduced, altered, or eliminated if regional climate trends continue (Parmesan *et al*. 2000, Araújo *et al*. 2004, Grayson 2005, Parmesan 2006). Changes in temperature and precipitation are likely to push some ecosystems, and the species inhabiting them, poleward or up-slope (McKenney *et al*. 2007, Virkkala *et al*. 2008, Thomas and Lennon 1999, Hickling *et al*. 2005), or cause contractions in their ranges (Hickling *et al*. 2006, Jetz *et al*. 2007, Lenoir *et al*. 2008). Asynchronous phenological responses to changing climate may break down inter-species interactions (e.g., plant-pollinator relationships), leading to short-term extinctions or extirpations (Parmesan *et al*. 1999, Beever *et al*. 2003). Combined with range-shifts and habitat alteration, these changes may exceed the physiological tolerances and phenotypic plasticity of species, which may cause further extinctions or extirpations (Reale *et al*. 2003, Berteaux *et al*. 2004). Novel interactions (e.g., predator-prey and competition) between previously isolated species may also cause extrinsic pressures that benefit certain species while

exceeding the ability of others to adapt to new environments and relationships.

The genetic variability existing within a species represents a fundamental level of biodiversity providing the basis for phenotypic variation and adaptation required to meet the demands of a changing environment (Vandergast *et al.* 2013). Identifying the current spatial distribution of genetic variation within a species is critical not only to inferring historic and ongoing evolutionary processes that have generated and maintained genetic diversity, but also central to identifying land use practices that are compatible with sustaining the evolutionary potential of species.

Analyses of landscape connectivity can provide a synthesis of habitat suitability, responses to climate change, and spatial patterns of genetic diversity. Such analyses are needed to quantify the importance of the spatial distribution of habitat for MGS dispersal and movement processes now and in the future. Even in the absence of predicted global change (climate change, urbanization and other development, invasive species, etc.), animal movement processes are critical for maintaining genetic diversity and for fostering species persistence through metapopulation processes, where local extirpation can be balanced through recolonization. Given global change predictions, maintenance of landscape connectivity is critical for allowing species to respond to changing habitat configurations. In concert with a variety of other land uses, current and planned energy developments not only threaten to reduce habitat area, but may impede the ability of MGS to move to suitable habitat as climate changes through the 21st Century and beyond.

Conflicts between large-scale renewable energy development in the western Mojave Desert and conservation of MGS habitat have delayed the establishment of energy facilities, and heightened the potential for costly litigation (e.g., NYT 2011). Analyses on the extent to which habitat may or may not be affected by proposed utility-scale renewable energy development are critically needed to reduce conflict among these competing land use interests, by guiding conservation planning and the effective siting of renewable energy projects and their supporting infrastructure. Informed and successful conservation planning depends on a robust procedure for habitat prioritization incorporating habitat suitability. This report provides analyses of past and current habitat suitability, how habitat may change in response to climate change, the spatial distribution of genetic diversity, and an analysis of habitat connectivity in relation to each of the previously mentioned factors. Following is a description of primary project objectives toward that end.

1.3 Objectives and Organization of Report

The following four primary objectives describe a research program sponsored by the California Energy Commission to provide information used in the resolution of some of the difficult issues described herein and to inform decision-makers representing public interests such as the Desert Renewable Energy Conservation Plan (DRECP; http://www.drecp.org) charged with balancing the need for landscape planning and conservation needs, while ensuring the harnessing of renewable energy resources.

Objective 1 was to provide a comprehensive and integrated analysis of MGS habitat in relation to previous development and planned renewable energy development using habitat suitability modeling. This objective is met in Chapter 2 entitled, "Is there room for all of us? Renewable energy and *Xerospermophilus mohavensis.*" To expedite the availability and use of this chapter to conservation and energy development planners in the region, this chapter was published as a Featured Article in the online peer-reviewed scientific journal: Endangered Species Research (Inman *et al.* 2013; http://www.int-res.com/abstracts/esr/v20/n1/feature/)

Objective 2 was to use the habitat suitability model developed in Chapter 2 to analyze future potential habitats relative to two climate change scenarios. To forecast potential climate change over time, the Intergovernmental Panel on Climate Change (IPCC) Assessment Report 4 outlined four future climate scenarios based on the potential for global change in terms of economic and human population growth, population demographics, consumption of fossil and alternative fuels, and technological development (IPCC 2001). The A2 and B1 climate scenarios (representing the largest and smallest expected changes in climate) were selected to evaluate the potential influence of climate change on the distribution of habitat for the MGS predicted for the year 2030 and 2080 in comparison to current conditions. Predictions of future habitat are compared to estimates of current habitat with consideration for the influences of proposed renewable energy development in the western Mojave Desert. In other words, to what degree does renewable energy development compound the problems associated with climate change?

Objective 3 was to establish the current state of knowledge concerning the geographic distribution of genetic diversity in the MGS by establishing both historic and ongoing factors that contribute to patterns of genetic variation within the species. Therefore, Chapter 4 begins with a broad geographic and deep temporal perspective. The focus is progressively narrowed to regional patterns of variation within the species, and ends with the most fine-scale view of factors contributing to the distribution of diversity within a particularly well-sampled population. Genetic information is linked to the habitat suitability and landscape connectivity data presented in earlier chapters of this report by examining if patterns of genetic distance are correlated with habitat-based distances among localities. Finally, a simulation approach is used to begin an examination of how various climate change scenarios might impact patterns of genetic diversity in this species. Throughout, efforts are made to maximize the use of information currently in hand, while identifying critical knowledge gaps and setting priorities for continued research. By evaluating genetic patterns across the landscape, in the absence of further development, inferences may be made regarding the relative influence of future development scenarios.

Objective 4 was to present a synthesis of the results for previous objectives coupled with a comprehensive spatial analysis of MGS landscape connectivity across the entire range of the species, under current conditions and various future scenarios representing climate change, genetic diversity, habitat connectivity, and energy development. In chapter 5,critical areas for connectivity are identified considering dual roles of habitat patches as sources of dispersers and as stepping-stone patches or key corridors. Hypothesized effects of land-use impacts influencing landscape connectivity are explored, including urban areas, roads, and agricultural lands. Important corridors are identified for facilitating MGS movement under current

conditions, as well as for facilitating distributional shifts in response to predicted climate change. Potential effects of planned energy development on MGS landscape connectivity, given current climate conditions as well as future climate change scenarios, are analyzed.

Chapter 6 synthesizes these four lines of evidence to draw general conclusions about the compatibility of the squirrels with renewable energy development within an evolving climate context. This information can be used in siting renewable energy projects with less impact on natural resources such as MGS and their habitats.

CHAPTER 2:
Is there room for all of us? Renewable energy and *Xerospermophilus mohavensis*

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2.1   Introduction

In recent decades the desert southwest region has seen some of the highest population growth in the United States, resulting in large-scale landscape modification and loss of habitat (Leu *et al.* 2008). Habitat loss and modification due to urban development, utility infrastructure, transportation corridors, military training, and recreational activities are occurring at an accelerating pace throughout the region (Lovich and Bainbridge 1999, Webb *et al.* 2009). Now the southwestern deserts are recognized as having great potential for renewable energy development given the availability of public land and abundant wind, solar and geothermal resources (NREL 2013). In recent years, public policy initiatives at both federal and state levels (e.g., the American Recovery and Reinvestment Act of 2009 and CA Executive Order S-14-08 and CA Senate Bill X1-2 among others) have mandated or encouraged the development of renewable energy.

One of the major benefits of increasing renewable energy generation includes reducing greenhouse gas emissions, thus mitigating global climate change; increasing national energy security; and supporting economic growth. The potential for renewable energy in the desert means that public lands in this region are now in great demand for development. However, the prospect of large-scale energy development and its associated infrastructure has raised serious concerns regarding impacts on desert biological resources, including many sensitive or protected species such as the desert tortoise (*Gopherus agassizii*; Fish and Wildlife Service 1990), the desert bighorn sheep (*Ovis canadensis nelsoni*; Fish and Wildlife Service 1998), and the Stephens' kangaroo rat (*Dipodomys stephensi*, Fish and Wildlife Service 1988), among others.

The Mohave ground squirrel (MGS; *Xerospermophilus mohavensis* Merriam) could also be impacted by the development of renewable energy resources. It is endemic to the western Mojave Desert in California, USA, and occupies portions of Kern, Los Angeles, Inyo and San Bernardino counties (Best 1995). The geographic range is thought to be approximately 20,000 km^2 (Hall 1981, Zeiner *et al.* 1988-1990) and is one of the smallest distributions among North American ground squirrels (Hoyt 1972, P. Leitner – *pers. obs.*). MGS occupy a harsh desert environment, and adult individuals are primarily active during a brief period from February to the end of July (Best 1995).

The restricted distribution of MGS, along with the extensive impacts of human development in the western Mojave Desert, has contributed to concern about conservation for this species (Leitner 2008). In particular, direct losses such as road and construction mortalities (Gustafson 1993) and the cumulative impacts (*sensu* Theobald *et al.* 1997) of landscape level disturbances (e.g., OHV, agriculture, military operations) could further reduce population numbers of MGS

and connectivity of suitable habitat patches. In response to these concerns, MGS was listed as Threatened under the California Endangered Species Act in 1984 (California Department of Fish and Game 2011). Although habitat loss has been identified as the greatest peril for MGS (Defenders of Wildlife and Stewart 2005, Fish and Wildlife Service 2011), a comprehensive, range wide assessment of habitat has not yet been published. Previous efforts to describe habitat have been qualitative, resulting in descriptions of habitat characteristics and multiple modifications to range maps (Zembal and Gall 1980, Hall 1981, Zeiner *et al.* 1988-1990). While these range maps provide useful information on the known extent of a species, they do not delineate areas of habitat and non-habitat within their extant range, which can be problematic when used for assessing areas of high biodiversity for conservation purposes (Pineda and Lobo 2012).

Conservation planning for many species has been facilitated by the use of species distribution models (SDMs) for tasks such as the design of conservation and monitoring programs, evaluating the efficacy or potential effects of management actions, and in recovery planning (Graham *et al.* 2004, Elith and Leathwick 2009a, Fish and Wildlife Service 2011). These SDMs, or habitat suitability models, are quantitative, spatially explicit models that relate species occurrence to environmental predictors thought to influence or define the suitability of habitat for the species (Franklin 2010, Peterson *et al.* 2011). These models can be ecologically complex or very simple, and can be modeled at many scales. Habitat models are frequently built with presence-only data (as absence data for most species are often unavailable), and provide a relative index of habitat suitability that can be predicted on a landscape scale.

Unfortunately, because SDMs have not yet been published for MGS, conservation and planning decisions have been made entirely on previously published range maps. In 2011, a petition for federal listing of the species (Defenders of Wildlife and Stewart 2005) was deemed not warranted by the US Fish and Wildlife Service on the basis of five factors (Fish and Wildlife Service 2011). One of these factors included "the present or threatened destruction, modification, or curtailment of its habitat or range", and in their ruling, FWS provided estimates of minimal habitat loss due to land use activities including, urbanization, agriculture and renewable energy. These estimates were based on range maps that were the best available information for planning purposes in lieu of SDMs. However, a larger percentage of habitat area has likely been lost in recent history than has been previously reported.

Conflicts between interests for large-scale renewable energy development in the western Mojave Desert and conservation of MGS habitat have delayed the establishment of energy facilities, and heightened the potential for costly litigation. Analyses on the extent to which habitat may or may not be affected by proposed utility-scale renewable energy development (USRED) are critically needed to reduce conflict between these competing interests, by guiding conservation planning and the effective siting of renewable energy projects and their supporting infrastructure. This report provides the first comprehensive and integrated analysis of MGS habitat conservation in relation to previous development and planned USRED using SDMs. The goal is to inform decision-makers representing public interests such as the Desert Renewable Energy Conservation Plan (DRECP; http://www.drecp.org) charged with balancing

the need for landscape planning and conservation needs, while ensuring the availability of renewable energy resources.

2.2 Materials and Methods

2.2.1 Study area

The study area covers 53,621 km^2 of the Mojave Desert in California including portions of Inyo, San Bernardino, Kern and Los Angeles counties, and encompasses the entire known historical range of MGS (Zeiner *et al.* 1988-1990). The region is characterized by desert mountain ranges and plateaus separated by lower elevation areas with geomorphic features such as washes, outwash plains, dry lakebeds, and basins. Though the study area included extremes in elevation, 99 percent of the entire study area was below 2,500 m. Regional precipitation ranges from 100 to 350 mm per year, with more rainfall occurring in the winter than summer (Hereford *et al.* 2004, Blainey *et al.* 2007) and at higher elevations. Temperatures range from below 0 °C in the winter months to over 54 °C in the summer with considerable daily and geographic variation (Turner 1994).

2.2.2 Species occurrence data

Locality records for MGS were compiled from the California Natural Diversity Data Base (CNDDB), the Mojave Desert Ecosystem Program, as well as recent trapping and survey work (P. Leitner and D. Delaney, *unpublished data*). Due to the low density of sampling and biased geographic distribution of observations, records dating back to 1975 were included to increase sample size. Records with known spatial uncertainty greater than 1 km (33 records) were excluded to keep the spatial precision of MGS observations similar to that of the environmental data layers, and the desired resolution of the habitat model (i.e., 1 km^2). Observations were limited to 1 per 1 km^2 grid cell, and incorporated a bias file to reduce the influence of biased geographic sampling (Phillips and Dudik 2008), which used a 4 km search radius from each observation record. After aggregating to the 1 km^2 grid size, there were a total of 440 observations for modeling.

2.2.3 Environmental data

The relationship between habitat suitability and covariate layers in a robust habitat model should ideally be explained by known ecological relationships between the organism of interest and its environment (Guisan and Zimmermann 2000, Elith and Leathwick 2009b). Eight environmental covariates were derived across the study area capturing known relationships between MGS and their environment (Table 1). These layers broadly represented climate (e.g., air temperature, precipitation, and climatic water deficit), land surface characteristics (e.g., topographic position and surface roughness) and the physical properties of the land surface (e.g., surface texture and albedo). The habitats that MGS occupy are generally flat, sandy or gravelly alluvial substrates with widely spaced shrubs (Burt 1936, Best 1995, Leitner 2008). Occupied vegetation types can include saltbush scrub, alkali desert scrub, creosote bush scrub, and yucca woodlands (Gustafson 1993, Best 1995). MGS are not, however, generally found on playas, rocky outcrops or other rocky surfaces such as desert pavement or boulder fields (Zembal and Gall 1980, Gustafson 1993). Because this work is also being used in parallel

analyses of the potential effects of climate change on MGS habitat suitability, only environmental covariates that could be projected to future dates under different climate change/global emission scenarios were used. Therefore, no measures of vegetation community or condition were included. While habitat suitability models derived without layers of key vegetation components of habitat may not represent the complete fundamental niche of a species, they can have acceptable predictive performance; for example, some of the initial models suggested only a 0.017 difference in the Area Under the receiver operator Curve statistic (AUC, Fielding and Bell 1997) between the best performing models that included vegetation layers and those without.

Table 1: Environmental variable names, abbreviations, study area means, standard deviations and descriptions

Name	Abbreviation	Mean	Std	Description
Precipitation	*precip*	195.3	161.0	Cumulative winter (October - March) precipitation, average of 30 years (1980 - 2010).
Surface Texture	*surface texture*	1103.5	205.0	The average difference in daytime and nighttime radiometric surface temperatures (Moderate Resolution Imaging Spectroradiometer MOD11A1 Land Surface Temperature 8-day Global 1 km data product) for the six 8-day periods from July 12th to August 29th for each year from 2000 to 2010. Higher values are indicative of sandy, smaller sized particles, while smaller values represent more rocky surfaces.
Surface Albedo	*surface albedo*	265.7	63.7	Average of summer (June - August) diffuse bihemispherical MODIS MCD43B3 16-Day L3 Global 1km Albedo data product for 2010.
Climatic Water Deficit (winter)	*winter cwd ave*	36.6	17.9	Average winter climatic water deficit, average of 30 years (1980 - 2010) for the months of October - March. High values represent greater evaporative demand on an area not met by available soil water.
Topographic Position	*Topidx*	8.7	2.1	Relative position of a given cell with respect to the potential for surface drainage. Calculated from USGS DEM. Higher values are indicative of dry lakebeds, valley bottoms and surface flow pinch points such as apexes of alluvial fans, while lower values represent ridgelines and mountaintops.
Probability of 3 year Drought	*drought prob3*	0.05	0.10	Proportion of the past 30 (1980 – 2010) years with consecutive 3-years with than 80 mm of cumulative winter precipitation.
Maximum Summer Air Temperature	*tmax*	30.78	5.28	Maximum of the monthly summer average (April - October) temperatures from past 30 years.
Surface Roughness	*SurfRuf*	1.03	0.05	Surface roughness index is calculated from USGS DEM (Hobson 1972). Higher values indicate a greater amount of surface terrain relief in a given area.

Climate covariates were obtained for the study area at a spatial scale of 270 m (Flint and Flint 2012), and included the 30-year mean for the winter months (October – March) of climatic water deficit (*winter cwd ave*), and cumulative winter precipitation (*precip*). Climatic water deficit was defined as potential evapotranspiration minus actual evapotranspiration, where actual evapotranspiration is the amount of water that evaporates from the surface and is transpired by plants. It is a measure of the evaporative demand on an area that was not met by available soil water, and is related to the amount of drought stress experienced by plants (Lenihan and Neilson 1993, Stephenson 1998). While often used to model the distribution of plant communities (see Huntley *et al.* 1995, Prentice *et al.* 1992), climatic water deficit is not often used in predictive models of vertebrates, due likely to the lack of widely available soil data required for its calculation. It is used here as a surrogate representing a potential limiting factor for vegetation. Potential evapotranspiration was defined as the total amount of water that can evaporate from the ground surface or be transpired by plants, and was calculated using a modification of the Priestly-Taylor equation (Priestly and Taylor 1972) as described in Flint *et al.* (2004).

Winter rainfall is important for the spring production of annuals (Beatley 1976, Turner and Randall 1989), and because MGS are generally only active from February to the end of July (Bartholomew and Hudson 1961, Hoyt 1972, Gustafson 1993, Harris and Leitner 2004), they require extensive foraging to sustain metabolic function throughout the year (Bartholomew and Hudson 1961). Areas with high spring production of annuals are therefore typically considered as habitat for this species. The probability of drought was estimated as the proportion of the past 30 years (1980 – 2010) during which 3 consecutive years had less than 80 mm of cumulative winter precipitation for a given 1 km^2 grid cell (*drought prob3*). Based on personal observations of MGS behavior and habitat condition, rainfall of less than 80 mm was selected to define drought conditions (P. Leitner, *pers. comm.*). A measure of air temperature was included as the 30-year mean for summer maximum temperature (*tmax*).

Layers related to land surface characteristics included *surface roughness* (Hobson 1972) and *topographic position* (described by others as "terrain wetness", Moore *et al.* 1991). *Topographic position* was used to represent the relative position of a given area with respect to the potential for surface drainage, and was calculated from the area of terrain that can drain into a given 1 km^2 grid cell. Higher values are indicative of closed basins, valley bottoms and surface flow pinch points such as apexes of alluvial fans, while lower values represent ridgelines and mountaintops. Elevation was not included as an environmental covariate due to its high correlation with several of the climate variables, and potential to complicate future climate scenario models.

Layers representing the physical properties of the surface substrate included an index of the particle size of the surface substrate (*surface texture*), which was derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) MOD11A1 Land Surface Temperature 8-day Global 1 km data products acquired from the Terra EOS AM satellite. This index was the average difference in daytime and nighttime radiometric surface temperatures for the six 8-day periods from July 12th to August 29th for each year from 2000 to 2010. The difference between the day and night surface radiometric temperatures is a function of the daily thermal inertia of

the surface substrate, which is a physical property of the substrate material and texture (Pratt and Ellyet 1979, Kahle 1987, Wang *et al.* 2004). Areas with dense rocky substrates have less daily fluctuation in surface radiometric temperatures than do areas with loose or sandy substrates (Kahle 1987). Summer, rather than winter temperatures were used due to the greater differences observed between day and night temperatures during this period (S. Nowiki, *unpublished data*). Higher values are indicative of sandy, smaller sized particles, while smaller values represent more rocky surfaces. Prior to calculating *surface texture*, surface temperature data were de-trended for elevation using a non-linear weighted regression.

Albedo of the surface substrate (*surface albedo*) was used from the MODIS MCD43B3 16-Day L3 Global 1km Albedo data product for the summer months as a measure of directional-hemispherical reflectivity of the surface material to represent dominant surface material types. *Surface albedo* is a primary determinant of the thermal properties of a surface material (Dickinson 1995), and is determined by the material type of the surface layer (Oke 1987). Prior to use in habitat models, all of the layers were re-sampled to the same 1 km² grid.

2.2.4   Data analyses

MaxEnt models were used (version 3.3.3e, Phillips *et al.* 2006) to develop a suite of candidate habitat models with up to five of the aforementioned environmental covariates. Each model was derived using 100 bootstrapped replicates with a random sample of 80 percent of the occurrences used for model training. Variables were excluded if their Pearson's correlation coefficient with other inputs was greater than 0.7. The resulting habitat models were first evaluated with an information theoretic approach using a modified Akaike's Information Criterion score that was bias corrected AICc for small sample sizes (Burnham and Anderson 2002). This metric was derived from the estimated log likelihood at all of presence locations (Phillips and Dudik 2008, Elith *et al.* 2011), where *k* was defined by the sum of all non-zero lambdas for a given model (Warren and Seilfert 2011). Models with parsimony were also evaluated for accuracy, goodness-of-fit and plausibility with several additional methods, including AUC, and Boyce Index (BI, Boyce *et al.* 2002), testing GAIN (GAIN represents the improvement in penalized average log likelihood over null model, *please see* Elith *et al.* 2011), as well as marginal and solitary response curves (Phillips and Dudik 2008). The AUC statistic was calculated from an internally withheld set of 20 percent of the MGS presence locations for each bootstrapped replicate, while the BI was estimated with all of the MGS observations. Prior to estimating the BI, each habitat model was rescaled to ensure that all models ranged from [0 - 1] by subtracting the minimum value and dividing by the difference of the minimum and maximum values.

Models containing any covariates with less than 10 percent contribution were removed from the suite of candidate models, favoring robust covariates over those with little contribution. The prediction surfaces for each model were checked to ensure that the predictions were not unrealistic, especially in areas where few data were available but some personal knowledge of habitat was available (P. Leitner). We selected the model that appeared closest to reality among the suite of candidate models to represent MGS habitat suitability. This model and its uncertainty were derived as the mean and standard deviation of the habitat suitability scores

across all 100 bootstrapped replicates. To gain insight into the key predictors defining habitat for MGS, environmental covariates that were most limiting with respect to habitat suitability throughout the study area were identified. The limiting variable was taken as the environmental covariate that provided the greatest increase in habitat suitability in a given pixel if the value for that variable was adjusted to the mean of the entire study area (Elith *et al.* 2010).

2.2.5 Anthropogenic Impacts

Current impacts to habitat from human development (urbanization, extensive road networks, and cleared or altered vegetation) were analyzed using three impact scenarios (High, Medium and Low). For each of these anthropogenic influences, separate scale factors were derived for the three impact scenarios with reduced habitat suitability in affected areas. Few data exist to suggest quantitative relationships between anthropogenic influences and MGS habitat degradation, and therefore the impact scenarios represent a range of uncertainty in the effects of habitat degradation rather than known and tested relationships. Scale factors were derived for each of the impact scenarios from expert opinion based on field observations. The High impact scenario uses scale factors representing the most extreme, yet plausible, degradation to MGS habitat, while the Low impact scenario represents an underestimate of degradation to MGS habitat. The Medium impact scenario was defined as the middle point between the High and Low impact scenarios. Combined, these three scenarios present a range of reasonable estimates of habitat suitability from least to most conservative, and can provide a bounded assessment of the status of habitat for land management purposes in light of anthropogenic influences.

Urban areas were derived from the National Land Cover Database (NLCD) 2006 Percent Developed Imperviousness layer, downloaded from the Multi-Resolution Land Characteristics Consortium (Fry *et al.* 2011). Grid cells with more than 20 percent of their surface area covered by at least 20 percent imperviousness were categorized as urban. The scale factors in urban areas for the three impact scenarios were as follows: High: 1.0, Medium: 0.75, Low: 0.30 (Table 2). In these areas, the product of the habitat suitability score from the scale factor was subtracted from the habitat suitability score for each cell. For example, in the High impact scenario, a cell with a habitat suitability score of 0.65 that was located in an area classified as urban, was modified by subtracting the product of the habitat suitability score (0.65) and the scale factor for urban areas (1.0) from the habitat suitability score (0.65), yielding a new habitat suitability score of 0. In the High impact scenario, it was assumed that urban areas present a complete loss of habitat, such that none of the essential resources (especially food and cover) are available. In contrast, the Low impact scenario represents the assumption that only a slight degradation of habitat has occurred in urban areas.

Table 2: Scale factors and suitable habitat for impact scenarios

Energy	Impact Scenario	Scale Factors						Suitable Habitat (Km^2)	% Loss of Historic
		Anthropogenic Influences			Renewable Energy Influences				
		Urban	Roads	Ag/Cleared Veg	Transmission Corridors	Wind	Solar		
None	Historic	*	*	*	*	*	*	19,023	*
	Low	0.300	0.100	0.500	*	*	*	17,139	9.9%
None	Med	0.750	0.250	0.750	*	*	*	16,525	13.1%
	High	1.000	0.400	1.000	*	*	*	15,927	16.3%
	Low	0.300	0.100	0.500	0.100	0.100	0.750	17,058	10.3%
USRED	Med	0.750	0.250	0.750	0.250	0.250	0.875	16,142	15.1%
	High	1.000	0.400	1.000	0.500	0.500	1.000	14,369	24.5%

Major roads were identified using U.S. Census Bureau Topologically Integrated Geographic Encoding and Referencing (TIGER) line files and assigned scale factors for each of the impact scenarios of: High: 0.4, Medium: 0.25, and Low: 0.10. While there is evidence to suggest direct mortality from vehicular traffic and the construction of new roads (P. Leitner, *pers. comm.*), recent work has shown that many small mammals exhibit neutral or slightly positive responses in abundance to the presence of roads and vehicular traffic (Fahrig and Rytwinski 2009). In the absence of data for MGS, scale factors that reflected the potential for only minimal impact to MGS habitat were used.

As with urban areas, places where land use activities have visibly altered or removed vegetation, such as agricultural or military activities, present significant degradation to MGS habitat. In addition to the direct loss of habitat, these activities may introduce insecticides, herbicides, and rodenticides to habitat (Hoyt 1972). These areas were digitized from recent remote sensing imagery where at least 90 percent of each grid cell showed evidence of altered or cleared vegetation. Here, scale factors of High: 1.0, Medium: 0.75, and Low: 0.5 were applied. Habitat suitability scores were reduced in these areas because of the importance of shrubs to MGS habitat (Best 1995).

Three types of anthropogenic impact were assessed on MGS habitat by categorizing habitat suitability into a binary representation of suitable and unsuitable habitat for each of the three impact scenarios using the 5th percentile of habitat suitability scores (0.438 was used as the threshold) for all of the cells with MGS occurrences (Liu *et al.* 2005). This resulted in the total area of suitable MGS habitat for each of the three scenarios, which were compared to the amount of suitable habitat predicted in absence of urban development, roads or cleared vegetation to provide a historical perspective of how much habitat might have existed prior to urbanization in the region.

2.2.6 Renewable energy

The extent and degree to which suitable MGS habitat will be affected by proposed USRED was evaluated by compiling a spatial representation of current and proposed renewable energy development on BLM lands in California from the Solar Energy Development Programmatic Environmental Impact Statement (BLM and DOE 2012). Areas designated as transmission corridors under the California Desert Conservation Area Plan of 1980 (BLM 1980), and the West-wide Designation of Energy Corridors (DOE and BLM 2008) were also included. Additional renewable energy projects (such as wind and geothermal sites) and their associated spatial footprints were identified and provided by the Renewable Energy Project Manager for the California Desert BLM District Office (G. Miller, 2011, Supervisory Projects Manager, Renewable Energy Coordinating Office California Desert District Bureau of Land Management, *unpublished data*). As with the urban impact scenarios, three scenarios of impact by USRED on MGS habitat were developed. Again, few data are available to quantify the relationship between USRED and degradation of MGS habitat; therefore expert opinion was used to derive scale factors. Recent work on California ground squirrel (*Otospermophilus beecheyi*) suggests that wind energy facilities can cause an increase in alert vocalizations and anti-predator vigilance behavior in individuals (Rabin *et al.* 2006), though estimates on the effects to their habitat or a

population are lacking. Similarly, transmission corridors are thought to have slight negative effects on many ground-dwelling species through the introduction of predators and exotic species (Stiles and Jones 1998, Gelbard and Belnap 2003), and alteration of vegetation communities (Loft and Menke 1984, Clarke *et al.* 2006, King *et al.* 2009). Due to the similarities in perceived degradation to MGS habitat between wind energy developments and transmission corridors, scale factors of 0.5, 0.3 and 0.1 were assigned for both disturbance types for the for the High, Medium, and Low renewable energy impact scenarios, respectively. It was assumed that solar energy developments have a greater impact to MGS habitat due to their extensive alteration of vegetation and soil characteristics (BLM and DOE 2012), and therefore assigned scale factors of 1.0, 0.875 and 0.75 for each of the High, Medium, and Low renewable energy impact scenarios, respectively. It is acknowledged that few data are available to quantify the impacts of USRED on MGS habitat, and therefore these scale factors are educated approximations, derived from observations of current USRED in locations outside the previously published range of MGS (Zeiner *et al*. 1988-1990).

To evaluate the extent and the degree to which MGS habitat could be affected by USRED the total amount of suitable habitat in each of the three USRED and urban development scenarios of impact were calculated. Separately, the means of habitat suitability scores in USRED (without the USRED impact scenarios) were compared with the remainder of the study area for each of the urban development scenarios of impact to identify if areas with proposed USRED have greater habitat suitability for MGS than the rest of the study area. The difference in suitable habitat influenced by solar and wind USRED was also calculated.

2.3 Results

2.3.1 Habitat models

The best overall model had four covariates and was selected from among 86 initial models that were evaluated. The best model was indicated by the lowest AICc score and an AIC weight of 1 included four environmental covariates. This model also had the highest AUC, and GAIN, and was among the higher performing models with respect to BI, although none of these performance measures indicated as strong a difference as the AIC evaluation (Table 3). The environmental covariates in the best model included: *surface texture*, *surface albedo*, *winter cwd ave*, and *precip*, with percent contributions of 46.6 percent, 25.4 percent, 16.3 percent and 11.6 percent respectively. Each of these environmental covariates describes a component of the broad habitat characteristics that were hypothesized to be important for MGS. These characteristics spanned climatic, topographic, and terrain features, and are related to the behavioral and physiological ecology of MGS.

Table 3: Performance measures and variable contributions of candidate models depicting habitat suitability for the Mohave ground squirrel.

Model	Npars	Performance Metrics				%Contribution							
		dAICc	AUC	BI	GAIN	ST	Alb	tpx	ruf	tmax	cwdWave	Prcp	ProbD3
ST+cwdWave+Alb+Prcp	4	0.000	0.888	0.950	1.133	46.6	25.4				16.3	11.7	
ST+cwdWave+Alb	3	77.755	0.864	0.949	1.000	51.1	29.0				19.9		
cwdWave+Alb+Prcp	3	94.367	0.863	0.968	0.977		55.9				26.1	18.0	
ST+Alb+Prcp	3	107.728	0.867	0.986	1.007	51.7	30.6					17.8	
ST+cwdWave+Prcp	3	114.677	0.867	0.878	0.987	65.8					20.2	14.0	
ST+tmax+cwdWave	3	124.178	0.863	0.959	0.959	66.4				14.4	19.2		
tmax+cwdWave+Alb	3	126.674	0.863	0.962	0.978		59.6			13.6	26.8		
cwdWave+Alb	2	138.860	0.858	0.976	0.949		63.8				36.2		
ST+cwdWave	2	158.554	0.858	0.878	0.939	72.2					27.8		
ST+tmax+Alb	3	181.443	0.854	0.946	0.923	56.8	31.4			11.8			
tmax+Alb+Prcp	3	191.524	0.856	0.939	0.915		61.8			12.1		26.1	
ST+cwdWave+Prcp+ruf	4	195.071	0.856	0.995	0.898	54.9			12.0		21.8	11.2	
ST+cwdWave+tpx+Alb	4	202.918	0.854	0.986	0.906	43.4	21.9	10.4			24.3		
Alb+Prcp	2	208.639	0.853	0.972	0.902		66.6					33.4	
ST+Alb	2	212.186	0.847	0.961	0.884	65.0	35.0						
ST+Prcp	2	213.360	0.847	0.925	0.875	74.0						26.0	
cwdWave+Alb+Prcp+ruf	4	218.721	0.850	0.967	0.885		45.3		13.0		29.6	12.2	
cwdWave+Alb+ruf	3	228.539	0.844	0.970	0.854		43.7		19.4		36.8		
tmax+Alb+Dprob3	3	241.093	0.841	0.958	0.853		67.0			19.0			14.0
cwdWave+tpx+Alb	3	242.998	0.840	0.995	0.835		41.6	21.3			37.1		
ST+cwdWave+ruf	3	247.529	0.847	0.964	0.845	56.7			12.6		30.7		
ST+cwdWave+tpx	3	252.644	0.845	0.961	0.843	55.1		16.0			28.9		
ST+tmax	2	258.912	0.833	0.928	0.804	77.6				22.4			
tmax+cwdWave+Prcp+ruf	4	259.315	0.848	0.970	0.842				40.3	13.9	35.3	10.5	
tmax+cwdWave+Prcp	3	259.593	0.850	0.951	0.858					27.2	41.2	31.7	
cwdWave+tpx+Prcp+ruf	4	262.753	0.842	0.965	0.804			33.7	14.9		37.1	14.3	
cwdWave+tpx+Prcp	3	274.594	0.840	0.946	0.807			46.2			39.8	14.1	
tmax+Alb	2	281.308	0.837	0.936	0.823		70.2			29.8			
Alb+Dprob3	2	291.562	0.830	0.986	0.777		82.0						18.0
tmax+cwdWave+tpx+ruf	4	294.414	0.835	0.978	0.792			32.7	15.9	13.4	38.0		
Alb+Prcp+ruf	3	294.605	0.838	0.990	0.799		48.9		19.3			31.8	
cwdWave+Prcp+ruf	3	296.035	0.839	0.966	0.806				44.7		40.8	14.5	
ST+tpx+Prcp	3	297.588	0.836	0.974	0.795	61.0		18.1				20.9	
cwdWave+tpx+ruf	3	297.593	0.837	0.993	0.803			35.8	16.2		48.0		
tmax+cwdWave+tpx	3	307.932	0.839	0.963	0.804			45.2		14.8	40.0		
tmax+cwdWave+ruf	3	309.179	0.832	0.950	0.757				43.2	18.3	38.5		
tmax+Alb+Prcp+ruf	4	314.627	0.833	0.986	0.774		51.1		18.0	10.8		20.2	
tpx+Alb+Prcp	3	322.969	0.832	0.998	0.777		44.8	26.2				28.9	
cwdWave+tpx	2	324.230	0.831	0.978	0.768			49.8			50.2		
ST+Prcp+ruf	3	331.655	0.833	0.971	0.767	69.3			10.5			20.2	
tmax+cwdWave	2	331.813	0.834	0.981	0.774					52.5	47.5		
tmax+Alb+Dprob3+ruf	4	332.233	0.831	0.987	0.782		49.0		20.1	11.2			19.7
ST+tmax+tpx+Dprob3	4	340.348	0.824	0.976	0.739	60.7		16.8		11.4			11.1
ST+tmax+Dprob3+ruf	4	341.030	0.828	0.984	0.761	65.4			12.2	11.8			10.7
tmax+tpx+Prcp+ruf	4	351.642	0.836	0.975	0.766			37.6	17.4	16.0		29.1	
ST+tmax+ruf	3	352.575	0.827	0.974	0.746	68.4			10.7	20.9			
cwdWave+Prcp	2	353.417	0.820	0.941	0.717						55.3	44.7	
tpx+Alb+Dprob3	3	353.948	0.821	0.978	0.735		50.9	25.5					23.7
tmax+Alb+ruf	3	357.057	0.822	0.993	0.723		50.9		23.0	26.1			
cwdWave+ruf	2	358.673	0.827	0.895	0.737				47.3		52.7		
tmax+Prcp+ruf	3	373.778	0.824	0.988	0.715				47.6	19.5		32.8	
Alb+Dprob3+ruf	3	374.048	0.815	0.971	0.708		55.2		19.9				24.9
tmax+tpx+Prcp	3	376.817	0.827	0.951	0.730			51.8		17.5		30.7	
tmax+tpx+Dprob3+ruf	4	378.634	0.819	0.980	0.710			41.1	18.1	19.4			21.4
ST+tmax+tpx	3	378.772	0.819	0.984	0.696	65.7		16.0		18.3			
tpx+Prcp+ruf	3	382.344	0.819	0.988	0.701			39.5	21.5			39.0	
ST	1	388.301	0.806	0.846	0.692	100.0							
tmax+tpx+Alb	3	389.155	0.819	0.982	0.722		46.6	28.0		25.5			
ST+Dprob3+ruf	3	395.182	0.808	0.960	0.678	71.1			16.4				12.5
ST+tpx+Dprob3	3	409.101	0.804	0.970	0.665	67.8		20.2					11.9
Prcp+ruf	2	412.172	0.812	0.968	0.663				55.2			44.8	
cwdWave+Dprob3	2	414.148	0.813	0.903	0.690						89.1		10.9
tmax+Prcp	2	418.926	0.808	0.936	0.649					49.9		50.1	
tpx+Prcp	2	428.142	0.813	0.936	0.669			55.6				44.4	

		Performance Metrics				%Contribution							
Model	Npars	dAICc	AUC	BI	GAIN	ST	Alb	tpx	ruf	tmax	cwdWave	Prcp	ProbD3
tmax+Dprob3+ruf	3	428.453	0.816	0.940	0.673				49.7	23.4			26.9
tmax+tpx+ruf	3	441.567	0.806	0.958	0.644			42.5	17.6	39.9			
tpx+Dprob3+ruf	3	442.947	0.799	0.953	0.629			48.4	20.9				30.7
Alb	1	443.962	0.805	0.964	0.651		100.0						
cwdWave	1	448.926	0.795	0.794	0.615						100.0		
tmax+tpx+Dprob3	3	450.012	0.799	0.970	0.620			54.2		20.5			25.3
ST+tpx	2	456.197	0.795	0.986	0.618	79.8		20.2					
ST+ruf	2	461.007	0.787	0.956	0.590	82.1			17.9				
tmax+tpx	2	462.108	0.799	0.978	0.613			57.9		42.1			
tmax+ruf	2	475.003	0.796	0.992	0.591				54.1	45.9			
tpx+Alb+ruf	3	493.642	0.794	0.970	0.596		64.1	24.6	11.3				
tpx+Dprob3	2	495.933	0.782	0.935	0.593			66.8					33.2
tpx+Alb	2	496.902	0.790	0.991	0.584		66.8	33.2					
tmax+Dprob3	2	499.091	0.793	0.978	0.606					72.1			27.9
Alb+ruf	2	525.527	0.787	0.959	0.557		73.6		26.4				
tmax	1	525.552	0.782	0.951	0.556					100.0			
Dprob3+ruf	2	541.217	0.787	0.938	0.569				66.2				33.8
Prcp	1	543.177	0.771	0.864	0.529							100.0	
tpx+ruf	2	651.202	0.750	0.967	0.403			68.3	31.7				
tpx	1	711.650	0.716	0.862	0.367			100.0					
ruf	1	727.974	0.724	0.853	0.328				100.0				
Dprob3	1	889.101	0.622	0.764	0.151								100.0

Performance measures included: Number of parameters (Npars), ΔAICc (dAICc), Area Under the receiver operating characteristic Curve (AUC), Boyce Index (BI) and testing gain (GAIN). Variable names are as follows: winter climatic water deficit (cwdWAave), cumulative winter precipitation (Pcp), summer maximum temperature (tmax), probability of 3 year drought (Dprob3), surface texture (ST), surface (Alb), surface roughness (ruf), and topographic position (tpx).

Marginal response curves for the environmental covariates in the selected model had patterns that were consistent with the hypotheses about their relationships to MGS habitat. Of the four environmental covariates, *surface texture* had the highest percent contribution at 46.6 percent. MGS habitat suitability peaked in areas where the difference between day and night surface radiant temperatures was between 25 and 30 °C, which was consistent with surface textures found in moderately coarse sandy soils. Habitat suitability decreased sharply when radiant temperature differences were below 20 °C (Figure 1), corresponding to areas with high proportions of large boulders and surface bedrock, and also in areas where differences were above 30 ºC, which are indicative of playas (primarily clay components) and extremely fine sandy surfaces. Surface texture was the limiting layer for 20,349 km^2 of the study area equating to approximately 45 percent of the area that was classified as unsuitable habitat (Figure 2). These areas included the majority of the mountains, foothills and rocky terrain in the study area, along with extensive areas of fine sand and silty, dry lakebeds.

Figure 1: Mohave ground squirrel marginal habitat model response curves.
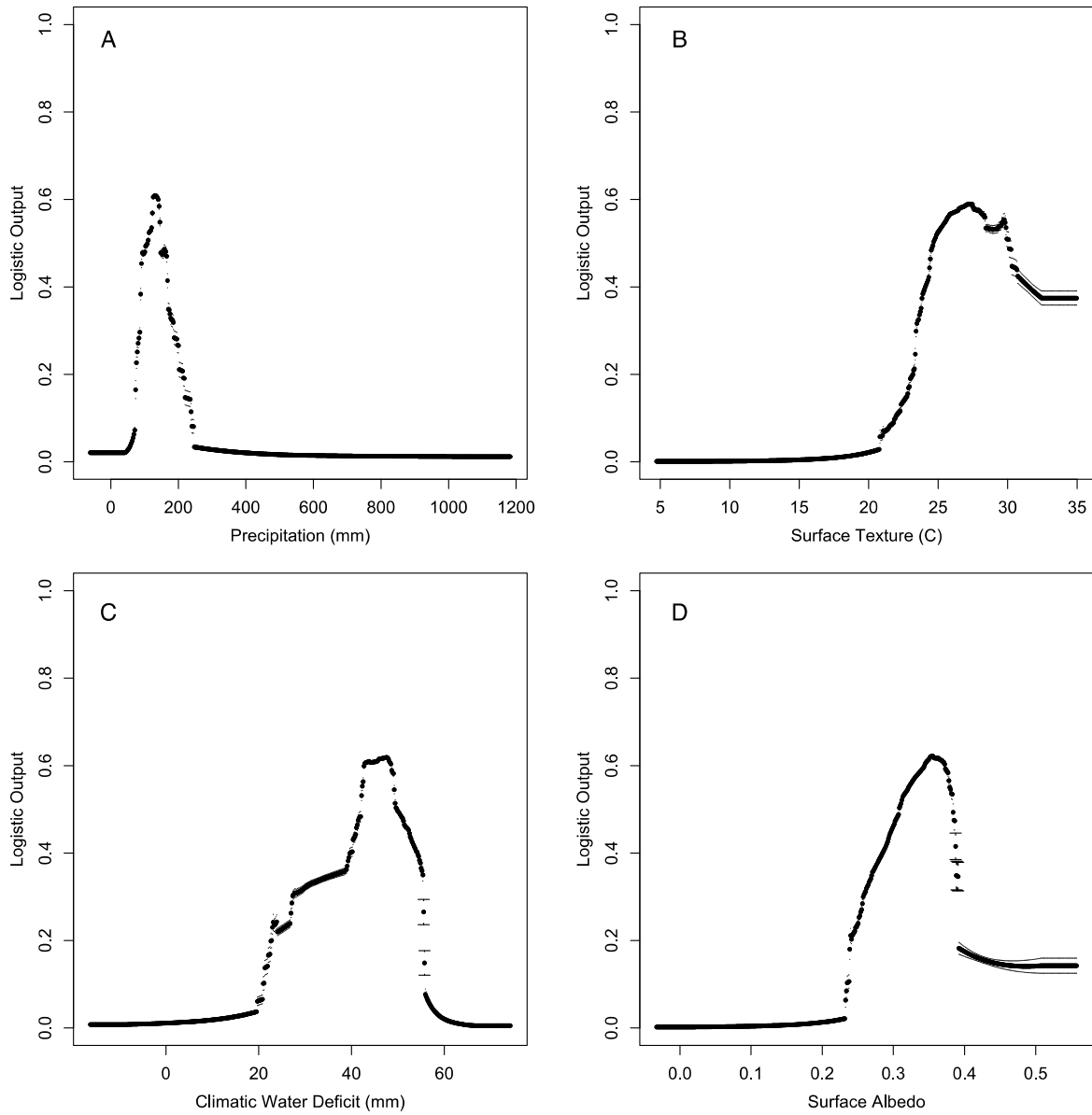
Starting from the upper left, A = Average Cumulative Winter Precipitation, B = Surface Texture, C = Average Winter Climatic Water Deficit, D = Summer Surface Albedo.

Figure 2: Limiting covariates in the selected habitat model for Mohave ground squirrel.
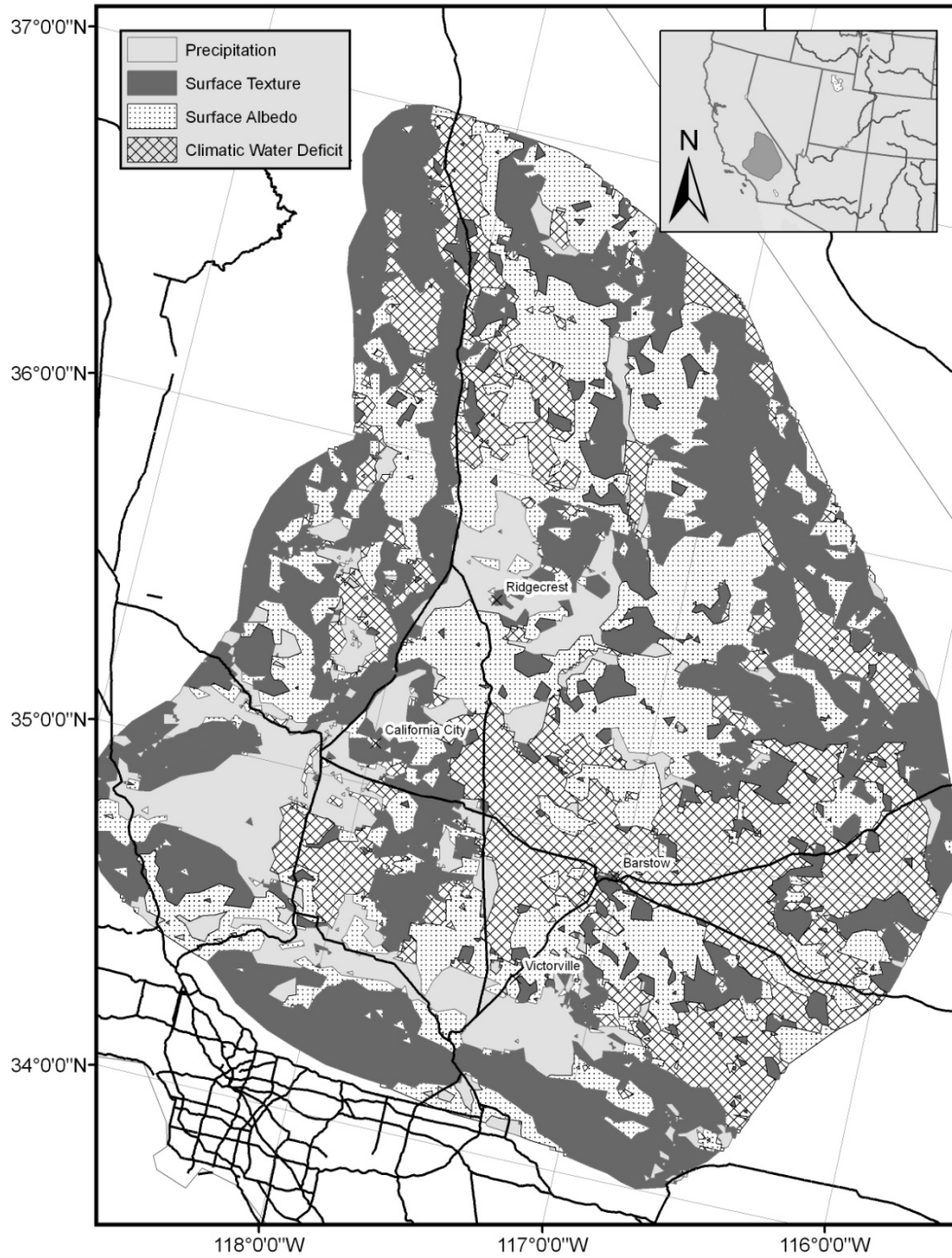
Areas where cumulative winter precipitation (light gray), surface texture (dark gray), albedo (stippled) and winter climatic water deficit (hashed) provided the greatest increase in habitat suitability if the value is adjusted to the mean of the entire study area. Urban, roads, and cleared vegetation areas are shown in black.

In contrast to *surface texture*, *surface albedo* provided a measure of the substrate material type, and differentiated substrates based on the proportions of incident solar energy that are absorbed by different soil types. *Surface albedo* had the second highest percent contribution at 25.4 percent, and showed a broad range (0.25 to 0.40) of values contributing to high habitat suitability (Figure 1) from the entire study area, which ranged from 0.16 to 0.52 (Figure 2). Only 27 percent (12,250 km^2) of unsuitable habitat was limited by surface albedo (Figure 2). MGS tended to occur in areas with higher albedo, as long as the substrates were not rocky or extremely sandy in texture. For example, areas with high albedo rocks in portions of the Red Rock Canyon State Park (southwest of Ridgecrest, CA) may appear suitable in terms of color and material, but due to their surface texture (extensive surface rock), they remained unsuitable. The same was true for many of the sand dunes present throughout the study area, where surface albedo suggested acceptable conditions, yet surface texture was too fine for MGS.

The percent contribution for winter climatic water deficit (*winter cwd ave*) was 16.3 percent. *Winter cwd ave* influenced habitat suitability over a relatively broad range of values found in the study area, with increased suitability occurring between 20 and 55 mm (60 percent of the study area), and a marked decrease in habitat suitability above 60 mm and below 20 mm of winter climatic water deficit (Figure 1). As a limiting layer, *winter cwd ave* covered 20 percent of the unsuitable areas (8,760 km^2; Figure 2), where average deficit was generally higher than 60 mm.

Precipitation had the lowest contribution of the four environmental covariates at 11.6 percent. MGS habitat exhibited a relatively narrow band of suitable values for *precip* (90 mm - 200 mm) when compared to the range of precipitation found in the study area (0 to nearly 1,200 mm). This narrow range of suitable precipitation values represented nearly 50 percent of the study area (Figure 1). As a limiting layer, *precip* represented only 9 percent of the unsuitable habitat (3,930 km^2; Figure 2), and in those areas, *precip* was higher than the average of suitable areas. Standard deviations of habitat suitability values across the 100 replicates ranged from nearly 0 to 0.206, with the highest standard deviations occurring in areas with moderate habitat suitability scores near the threshold used to distinguish suitable and unsuitable habitat (Figure 3). Areas with the highest standard deviations occurred directly to the west of Barstow, CA (Figure 3), and tended to have very fine surface texture and high surface albedo (Figure 1).

Figure 3: Model Standard Deviation map.
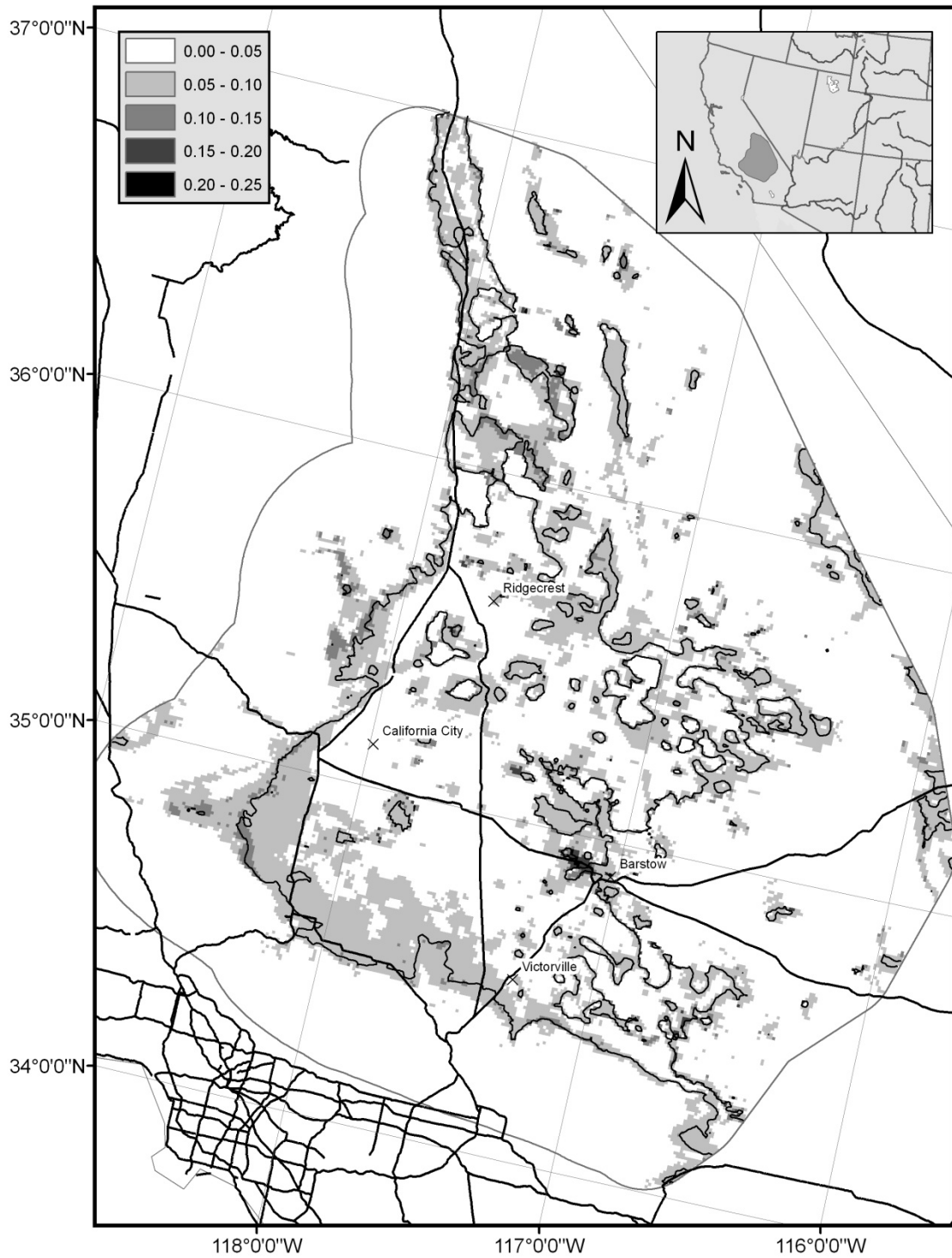
Darker colors represent areas with high standard deviations among the 100 bootstrap replicates. The model was based on 440 input localities. Modeling was conducted at a scale of 1 km (raster cell size = 1000 m). The threshold between suitable and unsuitable habitat is shown as a contour.

2.3.2 Impact scenarios

The initial habitat suitability model only accounted for natural features of the environment (i.e., in the absence of post- European disturbances), and predicted 19,023 km^2 of suitable habitat. The amount of suitable habitat under those conditions was compared to the three urban development scenarios of impact to evaluate potential habitat losses due to urban development. The potential habitat was reduced to 15,927 km^2, 16,525 km^2 and 17,139 km^2 for the High, Medium, and Low scenarios, respectively (Table 2). These scenarios estimate that somewhere between 1,884 km^2 (9.9 percent) and 3,096 km^2 (16.3 percent) of predicted suitable habitat have already been lost to the development of urban areas, roads and cleared vegetation during recent human settlements in the region.

The addition of proposed USRED indicates the potential to further reduce suitable habitat to 14,369 km^2, 16,142 km^2 or 17,058 km^2 for the High (Figure 4a), Medium, and Low scenarios of USRED impact. This represents an additional loss of 1,558 km^2 (9.8 percent), 383 km^2 (2.3 percent), and 81 km^2 (0.5 percent) of suitable habitat over the three urban development scenarios of impact. When added to losses due to current levels of development, this represents an overall loss of 24.5 percent, 15.1 percent and 10.3 percent of suitable habitat from potential pre-European development levels.

Figure 4: Suitable habitat (white) for Mohave squirrel under the High human development impact scenario (A; left) and historic habitat suitability without consideration for urban, roads, or cleared vegetation (B; right).
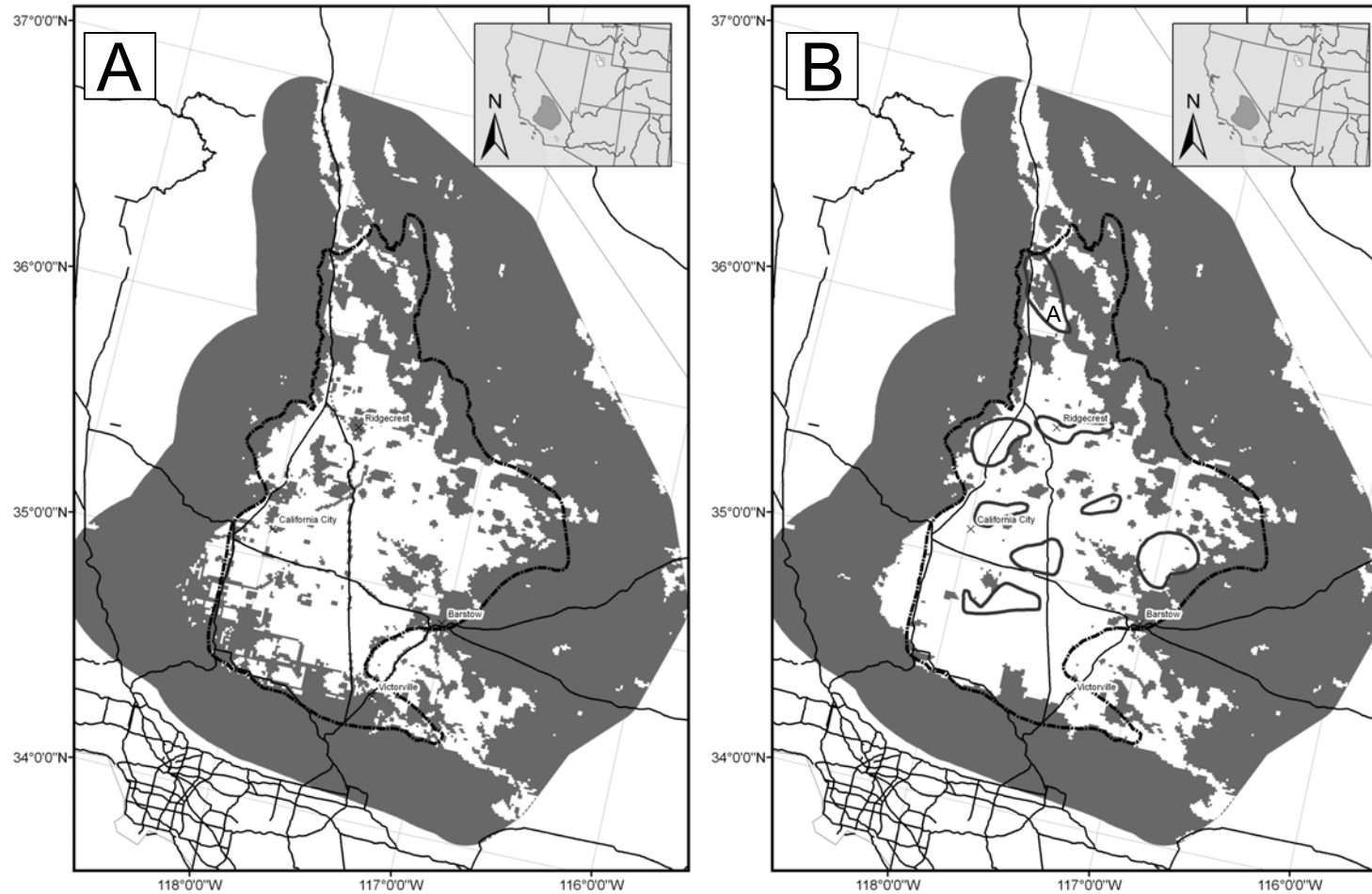
Of the three human development scenarios impact, the High scenario represents the greatest level of impact to MGS habitat due to impermeable surfaces, major roads, and cleared vegetation. The product of the corresponding habitat suitability score and a scale factor score (1.0, urban; from 0.4, roads; and 1.0 vegetation) were subtracted from the habitat suitability score. Habitat suitability scores for areas of proposed Utility-Scale Renewable Energy Development projects (USRED) were also reduced using scale factors of 0.5 for transmission corridors and wind facilities, and 1.0 for solar facilities in the High scenario. Core areas (B; right; Leitner 2008) are outlined in black. The MGS range map (Zeiner et al. 1988-1990) is outlined in hashed-black on both maps, while major roads are shown for reference only (black).

The average habitat suitability score was higher by 0.077, 0.081, and 0.093 in areas with proposed USRED than the rest of the study area for each of the three scenarios, (High, Medium, Low) respectively. This suggests that areas proposed for USRED are located in areas of high suitability habitat. When the amount of suitable habitat in the different types of proposed USRED (wind vs. solar) were compared, the difference was substantial, with only 2 km^2 of suitable habitat in proposed solar development in each of the three urban development scenarios of impact, and 503 km^2, 508 km^2 and 522 km^2 of suitable habitat in areas of proposed wind development for the three urban development scenarios of impact.

2.4   Discussion

Overlaying predicted habitat for the MGS with the human development scenarios of impact indicates that somewhere between 10 percent and 16 percent of historic suitable habitat has been lost to urbanization to date. The potential impacts of proposed renewable energy development were evaluated using three scenarios of potential impact, which predicted additional losses of 1 percent to 10 percent of historic suitable habitat for MGS, or a potential loss of up to 24 percent of suitable habitat within recent history. However, this is likely an underestimate of the potentially impacted area, because the model of habitat is estimated across all land ownership categories, while only public lands were evaluated to estimate the footprint of USRED. On state and private lands, 260 km^2 in the region have proposals for USRED, and an additional 3,500 km^2 may potentially be available for USRED (Fish and Wildlife Service 2011). The model of habitat indicates that there is potential for renewable energy development to impact nearly as much habitat as has been disturbed by human expansion into this region previously, equating a loss of up to a quarter of suitable habitat from pre-European settlement levels within the last century.

Encroachment of urban areas on MGS habitat introduces several modes of habitat disturbance including off-highway vehicles, roadways, airports and high-voltage transmission lines (Leitner 2008) that affect habitat and populations of flora and fauna in a variety of ways. Additional USRED in the region will increase the need for more transmission lines and associated roads, and combined with the energy facilities themselves, loss of habitat and other impacts to species may occur from site preparation and construction of buildings and access roads (Kuvlesky *et al.* 2007). Other changes to habitat may be caused by soil mixing or soil compaction, or the release of chemicals such as dust suppressants, dielectric fluids and herbicides throughout the operational life of the facility (BLM and DOE 2012). Separately, the alteration of surface water flow and increased erosion may cause changes in habitat productivity and the distribution of resources (Schwinning *et al.* 2011).

Transmission corridors tend to alter the vegetation community and structure of adjacent land, and therefore affect habitat through these vegetation alterations (Anderson *et al.* 1977, Johnson *et al.* 1979, Loft and Menke 1984, Clarke *et al.* 2006, King *et al.* 2009). These corridors may be permeable or even facilitate movement in some species, but may represent barriers to movement and dispersal for others (Schreiber and Graves 1977, Carthew *et al.* 2009). The influence on habitat and populations may also be larger than the physical footprint of USRED because human activities and the physical structures tend to provide resource subsidies such as

food, cover and water to native and invasive predators (Lovich and Bainbridge 1999). Transmission corridors and roads may also act as conduits for exotic and invasive species (Stiles and Jones 1998, Gelbard and Belnap 2003). For example, powerlines, roads and other linear right-of-ways provide nesting and perching sites for predatory birds, including common ravens (*Corvus corax;* Kristan and Boarman 2003, Coates *et al.* 2008, Peery and Henry 2010). Ravens (*Corvus corax*) and coyotes (*Canis latrans*), subsidized by human activities, can have detrimental effects on native wildlife in proximity to urban locations (Lovich and Bainbridge 1999, Boarman 2003, Esque *et al.* 2010). While increased predation on native wildlife has caused population losses in other species, and is likely to similarly impact MGS populations, research is needed to quantify the landscape-wide effects of urbanization on MGS populations.

The long-term effects of renewable energy development on MGS populations are also not well understood. Potential effects are complicated by differences between wind, solar, geothermal and other sources of USRED. The diffuse distribution of wind turbines with relatively undisturbed habitat among turbine bases has been suggested as not harmful and may even provide cover for desert tortoises (Lovich *et al.* 2011). However, the impacts of wind energy development on other desert wildlife, including MGS, are not well understood (Lovich and Ennen 2011). In other studies, wind energy facilities have been shown to elicit increased alert vocalizations and anti-predator vigilance behavior in the California ground squirrel (*Otospermophilus beecheyi*) due to the addition of wind turbine prop-noise to their environment (Rabin *et al.* 2006). A review of acoustical interference in wildlife has shown negative population effects across a wide range of taxa including mammals, birds, amphibians, reptiles and even some invertebrates (see Chan and Blumstein 2011 for review), with the majority of effects manifesting as interference to communication between individuals, increased energy expenditures on predator avoidance, and population decline. The effects of wind and solar energy development on MGS behavior and population dynamics are not well understood and are important areas for research.

To illustrate the utility of the habitat model for regional planning purposes, the model was compared to a previously published range map (Zeiner *et al.* 1988-1990) and core habitat areas (Leitner 2008). The previously published range for MGS represents a hypothesis for the historical range and extent of MGS in the western Mojave Desert, and has served as a guide for implementing conservation strategies in the western Mojave Desert (BLM 2005) and the foundation for the 2011 FWS decision to deny MGS listing under the Endangered Species Act. The model of MGS habitat illustrates that many areas within the extent of the previously published MGS range map are not suitable as habitat for MGS (Figure 4a), and that much of the northern and eastern portions of the previously published range map contain unsuitable habitat. When applied to conservation, these differences in geographic area represent substantial differences between estimates of the amount of habitat that will be affected by USRED. In their 2011 decision, the FWS suggest that up to 6 percent of the MGS range may be affected by USRED on public and private lands, while in contrast, the High impact scenario suggests that up to 10 percent of current habitat will be negatively affected by USRED just on public federal land. With an additional 3,500 km^2 of state and private land in the study area, the amount of MGS habitat affected by USRED may be substantially higher.

Some areas are identified with suitable habitat outside the MGS range map (see below), though these areas have never been surveyed for MGS, and may represent uninhabited areas that have not been colonized. Such areas include suitable habitat farther north in the Owens Valley than was previously thought, as well as farther south and east of Apple Valley than was previously published. Unlike the previously published range map, the published core areas represent areas where populations of MGS have been detected for multiple years in large (>30) numbers at multiple trapping sites (>6; Leitner 2008). These areas are thought to represent population centers, and have been suggested as key areas for MGS conservation (Leitner 2008). In general, these core areas overlapped some of the highest habitat suitability, although the northern most core area encompassed lower habitat suitability than the others (area "A" in Figure 4b). This core area was designated due to the high numbers of MGS trapped at its most northern and southern end, though few MGS have been observed in its central region.

One proposed USRED in particular was noted in an area of high suitability habitat located northwest of Red Rock Canyon State Park, and approximately 30 km south and west of Ridgecrest, CA. In addition to high suitability habitat, this area has some of the highest densities of trapping records, may serve as an important corridor for dispersal among populations (Weisberg *et al. unpublished data*), and is a region of high genetic variation that harbors one of three distinct genetic groups within the species (Bell and Matocq 2011). Siting future USRED away from areas with high suitability habitat may promote MGS population persistence.

2.4.1 Model error

Identifying areas where habitat models provide less certainty about their predictions of habitat suitability is critical for land use planning purposes, because of the consequences to conservation if unsuitable habitat is conserved instead of suitable habitat. For example, if the reliance on erroneous habitat suitability models leads to the siting of land use activities that are incompatible with conservation on remaining MGS habitat, regional planning efforts will be unable to meet conservation goals. It is critical, therefore, to acknowledge and understand model error and model bias when interpreting and incorporating model predictions into planning efforts. Others have also suggested that error maps be included with all habitat models, regardless of the methods used to create them (Rocchini *et al.* 2011). Doing so will promote awareness that no model is absent of error or bias.

Estimates of model uncertainty are evaluated throughout the study area to identify locations where the model yielded greater uncertainty about predictions of habitat suitability (Figure 3). These areas were identified for their high variation in model prediction among the 100 training iterations (each with a random selection of 80 percent of observations). While the greatest uncertainty occurred in a valley directly to the west of Barstow, CA (Figure 3), high uncertainty was also identified in areas with very fine surface texture and high surface albedo. These areas tended to have moderate habitat suitability scores near the threshold for delineating suitable and unsuitable habitat. This suggests that the model predicts high suitability scores and low suitability scores with greater precision than it does moderate suitability scores, and that the transition between unsuitable and suitable habitat is less certain than either of the extremes.

Among the factors contributing to this error were the multiple sources of observation data, each with its own pattern of geographic bias due to non-random sampling. This bias has been shown to influence the perceived relationship between a species and its environment (Hortal *et al*. 2008, Soberon and Nakamura, 2009), thereby compromising the ability to quantify the ecological niche for a species. However, there was less concern with the ability to quantify the ecological niche of MGS than with developing a predictive, yet biologically plausible, model for the current geographic distribution of MGS habitat. Another source of error was the temporal span of the input observations, which dated back to 1975 to increase sample size. However, because of the rapid human population growth in the past several decades, locations for some of the observations are now in areas with urban development or agriculture. Potential bias was removed from these land use changes by limiting the environmental covariates to those that have remained relatively unchanged by land use over the past 30 years

Two easily discernible conditions were identified across the landscape where additional sampling could improve future habitat models and benefit conservation planning for MGS. The first included areas with moderate to high suitability scores with no evidence of MGS presence, and the second included areas with high model error, as shown in Figure 3. Areas that met the first condition likely occurred because of one of three reasons: 1) the model predicted high suitability habitat and sampling did not occur, 2) the model predicted high suitability habitat and sampling did occur, but no MGS were detected even though they were present, and 3) the model predicted high suitability habitat and sampling did occur, but MGS were not detected and were not present. The first provided the single largest amount of sample selection bias, due to a lack of random (or stratified random) sampling over large areas of potential habitat, which confounds the distribution of sampling effort with the true species distribution (Hortal *et al*. 2008, Soberon and Nakamura, 2009). These areas were indistinguishable from those where sampling occurred, but no MGS were detected (reasons 2 and 3), because absence data were not available. Absence data require the use of repeated presence-absence surveys to estimate the probability of detection (MacKenzie *et al.* 2002), which is needed to estimate the confidence or reliability of absence data (Mackenzie *et al.* 2005, Kery *et al.* 2010, Graham *et al.* 2004). Camera trapping surveys for MGS were designed to obtain presence-absence data and have recently been implemented (P. Leitner and D. Delaney, *pers. comm.*), though few data are available for modeling. Areas meeting the second condition for additional sampling included areas with high model error, which are shown in Figure 3. Continued and increased sampling efforts are recommended in areas that meet these two conditions, especially in areas where sampling has not yet occurred and are predicted to have moderate to high suitability habitat. In particular China Lake Naval Air Weapons Center encompasses areas of high suitability habitat (>0.7), yet has had little sampling. This military installation also includes some of the most northerly predictions of suitable habitat, and it will be important for interpreting conservation issues such as conservation genetics, habitat connectivity, and MGS responses to climate change.

2.4.2 Tools for conservation

Habitat suitability modeling has provided a new status-of-knowledge for MGS that managers can use to make informed decisions about resource management in or near MGS habitats. This model makes it possible to provide quantitative estimations of historical habitat availability,

current suitable habitat availability, species use and connectivity across landscapes, and to predict trends in the availability of habitat based on resource management plans. Sound resource management decisions depend on reliable habitat, population and threats information. As the most complete current understanding of suitable habitat for this species, this model provides a valuable planning resource, but equally important, the model helps identify critical areas in need of research to strengthen future modeling efforts for this species.

CHAPTER 3:
Impacts of climate change and renewable energy

By Richard D. Inman, Todd C. Esque, Kenneth E. Nussear, Philip Leitner, Marjorie D. Matocq, Peter J. Weisberg, and Thomas E. Dilts

3.1   Introduction

The influence of climate on species distributions has been studied extensively, with many clear relationships between regional climates and the distribution and diversity of species (Pianka 1966, Woodward 1987, Campbell *et al*. 2009). However, the consequences of a changing climate are still a topic of much research, with some studies suggesting that the distributions of many North American flora and fauna species will be reduced, altered, or eliminated if regional climate trends continue (Parmesan *et al*. 2000, Araújo *et al*. 2004, Grayson 2005, Parmesan 2006). Changes in temperature and precipitation are likely to push some ecosystems, and the species inhabiting them, poleward or up-slope (McKenney *et al*. 2007, Virkkala *et al*. 2008, Thomas and Lennon 1999, Hickling *et al*. 2005), or cause contractions in their ranges (Hickling *et al*. 2006, Jetz *et al*. 2007, Lenoir *et al*. 2008). Asynchronous phenological responses to changing climate may break down inter-species interactions (e.g., plant-pollinator relationships), leading to short-term extinctions (Parmesan *et al*. 1999, Beever *et al*. 2003). Combined with range-shifts and habitat alteration, these changes may exceed the physiological tolerances and phenotypic plasticity of species, which may cause further extinctions (Reale *et al*. 2003, Berteaux *et al*. 2004). Novel interactions (e.g., predator-prey and competition) between previously isolated species may also cause extrinsic pressures that benefit certain species while exceeding the ability of others to adapt to new environments and interactions. Further complicating these stressors, surface-disturbing land uses (e.g., urbanization, transportation corridors, military training, agriculture, and recreational activities) have altered vast areas of the landscape (Leu *et al*. 2008), fragmenting habitat, and disrupting habitat corridors, thus potentially restricting the ability of species to migrate to new areas (McInerny *et al*. 2007, Wilson *et al*. 2010).

To forecast how climate may change over time, the Intergovernmental Panel on Climate Change (IPCC) Assessment Report 4 outlined four emissions scenarios based on the potential for global change in economic and human population growth, population demographics, consumption of fossil and alternative fuels, and technological development (IPCC 2001). These emissions scenarios provide a set of greenhouse gas (GHG) constraints under which Global Climate Models (GCMs) can derive projections of future climate conditions. The A2 and B1 emissions scenarios (representing medium-high, and low emissions, respectively) were coupled with the NOAA GFDL CM 2.1 GCM to evaluate the potential influence of climate change on the distribution of habitat for the Mohave ground squirrel (MGS; *Xerospermophilus mohavensis* Merriam). The conditions forecast by these two climatic scenarios (GFDL A2 and GFDL B1) are applied to the previously developed model of MGS habitat (hereafter, current conditions model, Chapter 2). Predictions of future potential habitat are compared to estimates of current habitat with consideration of the influences of proposed utility-scale renewable energy development (USRED) in the western Mojave Desert. The descriptions of USRED and the MGS current

conditions model from Chapter 2 were used for the analyses in this chapter.

3.2   Materials and Methods

3.2.1 Study Area

To examine the influences of climate change, the study area was enlarged from 53,621 km^2 (used in Chapter 2) to 118,872 km^2 of the Mojave Desert and Great Basin ecoregions in California and Nevada. The additional area was added to accommodate predicted MGS habitat distributions under the future climate scenarios, which extended to the north of the study area used in Chapter 2.

3.2.2 Environmental Data

Four environmental variables were used to model habitat for the MGS (Chapter 2). Two of the variables, surface texture (*surface texture*), and surface albedo (*surface albedo*), depend on the geomorphic surface across the landscape and thus were assumed to persist in their current state over decadal time frames. In contrast, the remaining two variables were predicted to change in response to the climate forecast under the two climatic scenarios. These were climatic water deficit (*winter cwd ave*) and cumulative winter precipitation (*precip*). Both variables were derived from downscaled GCM predictions produced by the NOAA GFDL CM2.1 model (Delworth *et al*. 2006, Stouffer *et al*. 2006), and are described in Flint and Flint (2012). The GFDL CM2.1 model was chosen because of its ability to predict a range of environmental conditions and a realistic representation of California's recent historical climate (Delworth *et al*. 2006) and because it was identified as producing a realistic representation of California's recent historical climate, including the strong seasonal precipitation cycles of the California desert region (Cayan et al. 2008). The GFDL CM2.1 model is generally more sensitive to slight variations in emissions scenarios and predicts warmer and drier climates than other GCMs reviewed by the IPCC (Cayan et al. 2006). Climatic water deficit was defined as potential evapotranspiration minus actual evapotranspiration, where potential evapotranspiration was defined as the total amount of water that can evaporate from the ground surface or be transpired by plants, and was calculated using a modification of the Priestly-Taylor equation (Priestly and Taylor 1972) as described in Flint *et al*. (2004). Winter precipitation was defined as the 30-year mean of winter precipitation (Oct – April). Climate change data were based on the GFDL A2 and GFDL B1 climatic scenarios (IPCC 2001) because they represent scenarios that bound conditions likely to produce extremes of future habitat for MGS. Predictions of MGS habitat were calculated for the years 2030 and 2080 using the average of the 30 years preceding each of these dates for the two climate variables.

3.2.3 Data Analysis

The current conditions model (Chapter 2) was used to predict habitat suitability under the GFDL A2 and GFDL B1 climatic scenarios for the years 2030 and 2080, resulting in four future predictions of MGS habitat. To account for alterations due to current land use the Medium anthropogenic impact scenario from Chapter 2 was used, including roads, urban areas, and areas with extensive habitat alteration due to agriculture or other surface disturbances such as

extensive cleared vegetation. Urban areas were derived from the National Land Cover Database (NLCD) 2006 Percent Developed Imperviousness layer (Xian *et al*. 2011), while major roads were extracted from U.S. Census Bureau Topologically Integrated Geographic Encoding and Referencing (TIGER) line files. Agriculture and extensive areas with cleared vegetation were identified using two different methods because digitized agriculture lands were not available for the larger study area. Within the areal extent of the current conditions model a spatial layer was derived from remote sensing and image interpretation as described in Chapter 2. Comparable layers depicting agricultural areas were derived from the National Land Cover Database 2006 (Fry *et al*. 2011) for the larger area required to accommodate future squirrel distributions in relation to future climate models. Current roads, urban areas, and areas with extensive habitat alteration were represented as spatial layers, and assigned scale factors (described in Chapter 2) to reduce habitat suitability where their influence occurred. Scale factors for urban areas, major roads, and agriculture were: 0.75, 0.25, and 0.75, respectively (see Chapter 2), and were used to reduce the habitat suitability value in impacted cells by subtracting the product of the habitat suitability score and the scale factor from the habitat suitability score.

Potential habitat under the GFDL A2 and GFDL B1 climatic scenarios was identified using a threshold to classify habitat suitability scores into a binary response using the 5th percentile of habitat suitability scores from the MGS observations used in the current conditions model (Liu *et al*. 2005). This threshold (0.295) was applied to the un-scaled logistic values from the MaxEnt predictions of habitat across the entire study area. The amount of current habitat lost under the two climatic scenarios is reported along with the net change in total habitat. Overlap between potential habitat under the GFDL A2 and GFDL B1 climatic scenarios was assessed to identify co-occurring areas of suitable habitat predicted for 2030 and 2080. It was assumed that because the two climatic scenarios have different predictions of future climate, any areas of overlap in predicted habitat are likely to be critical areas for future conservation of MGS.

To assess the potential for MGS to shift their range in response to climate change, an annual movement rate was applied to current (ca. 2000 to 2010) locations of MGS populations identified by field surveys (see Chapter 2). The rate (3 km per year) was estimated from known dispersal rates of juvenile MGS (Harris and Leitner 2005). It was assumed either that a population could move in any direction, or not at all. The potential area that could be occupied by MGS in 2030 or 2080 was assessed by limiting potential habitat to the areas that could be reached if individuals moved from their current populations at this rate. While this dispersal model is likely an oversimplification of the mechanism by which species' ranges shift (for example, no measures of resistance or barriers to movement such as terrain features, local weather fluctuations, squirrel demographics, or anthropogenic barriers such as roads, agricultural lands were included), it provides a simple method for distinguishing areas that may represent potential habitat in terms of the four covariates used in the current conditions model (dispersal-limited habitat) versus areas that possibly could support squirrels but squirrels may never access because of the conditions defined for this model scenario (inaccessible).

Finally, predictions of future MGS habitat were cast in light of proposed USRED for the region. A spatial representation of current and proposed renewable energy development on BLM lands was compiled for California and Nevada from the Solar Energy Development Programmatic Environmental Impact Statement (BLM and DOE 2012). Areas designated as transmission corridors under the California Desert Conservation Area Plan of 1980 (BLM 1980), and the West-wide Designation of Energy Corridors (DOE and BLM 2008) were also included. Additional renewable energy projects (such as wind and geothermal sites) and their associated spatial footprints were identified and provided by the Renewable Energy Project Manager for the California Desert BLM District Office (G. Miller, 2011, Supervisory Projects Manager, Renewable Energy Coordinating Office California Desert District Bureau of Land Management, *unpublished data*) and Southern Nevada BLM District Office (G. Helseth, 2011 Program Manager, Southern Nevada District Office, *unpublished data*). Scale factors (described in Chapter 2) were assigned to reduce habitat suitability where the USRED would occur. Scale factors for transmission corridors, wind USRED, and solar USRED were: 0.30, 0.30, and 0.875, respectively, and were used to reduce the habitat suitability score in impacted cells by subtracting the product of the habitat suitability score and the scale factor from the habitat suitability score. The degree to which future potential habitat could be affected by USRED was evaluated by calculating the total amount of potential habitat predicted by the climatic scenarios after each of the scale factors had been applied. Separately, the mean of habitat suitability scores in areas with USRED (without the USRED impact scenarios) was compared to the mean of habitat suitability scores for the remainder of the study area to identify if areas with proposed USRED will have greater habitat suitability under the two climatic scenarios. Areas of conservation concern exist where potential habitat under the two climatic scenarios overlaps with areas where USRED are proposed.

3.3 Results

3.3.1 Potential Future Habitat

The changes in climate under the GFDL A2 and GFDL B1 climatic scenarios for 2030 resulted in predicted losses of 9,422 km^2 (57.0 percent; Figure 5) and 8,617 km^2 (52.1 percent; Figure 6) of current habitat, respectively (Table 4). By 2080, losses of current habitat of 13,863 km^2 (83.9 percent; Figure 7) and 13,875 km^2 (84.0 percent; Figure 8) are predicted (Table 4). However, the climatic scenarios also resulted in additional habitat beyond the current range of MGS, with 7,876 km^2 and 8,151 km^2 of additional habitat (Table 4) predicted by 2030 for the GFDL A2 and GFDL B1 climatic scenarios, respectively. This additional habitat contributed to a total of 14,986 km^2 and 16,051 km^2 of potential habitat by 2030 for the two climatic scenarios, equating to a net loss of 1,539 km^2 and 474 km^2 of habitat, respectively. By 2080, the two climatic scenarios resulted in substantially less potential habitat, with a total of 8,852 km^2 and 8,973 km^2 of potential habitat across the region (Table 4).

Figure 5: Mohave ground squirrel habitat under the GFDL A2 climate scenario in 2030.
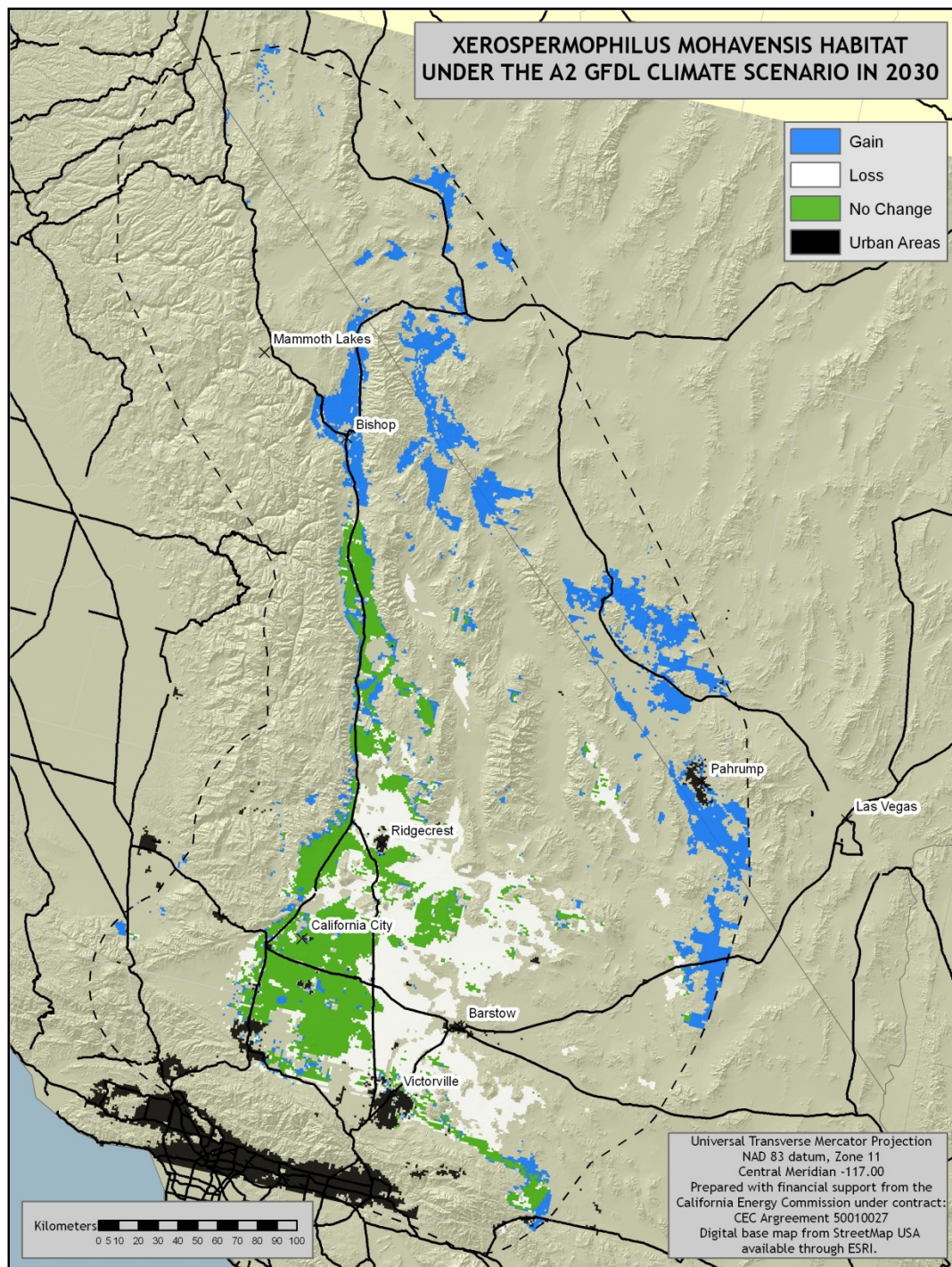
Current habitat that is predicted to remain habitat in 2030 is shown (green), while current habitat that is predicted to become unsuitable is shown in white. New habitat is shown in blue. The study area is shown with a dashed line.

Figure 6: Mohave ground squirrel habitat under the GFDL B1 climate scenario in 2030.
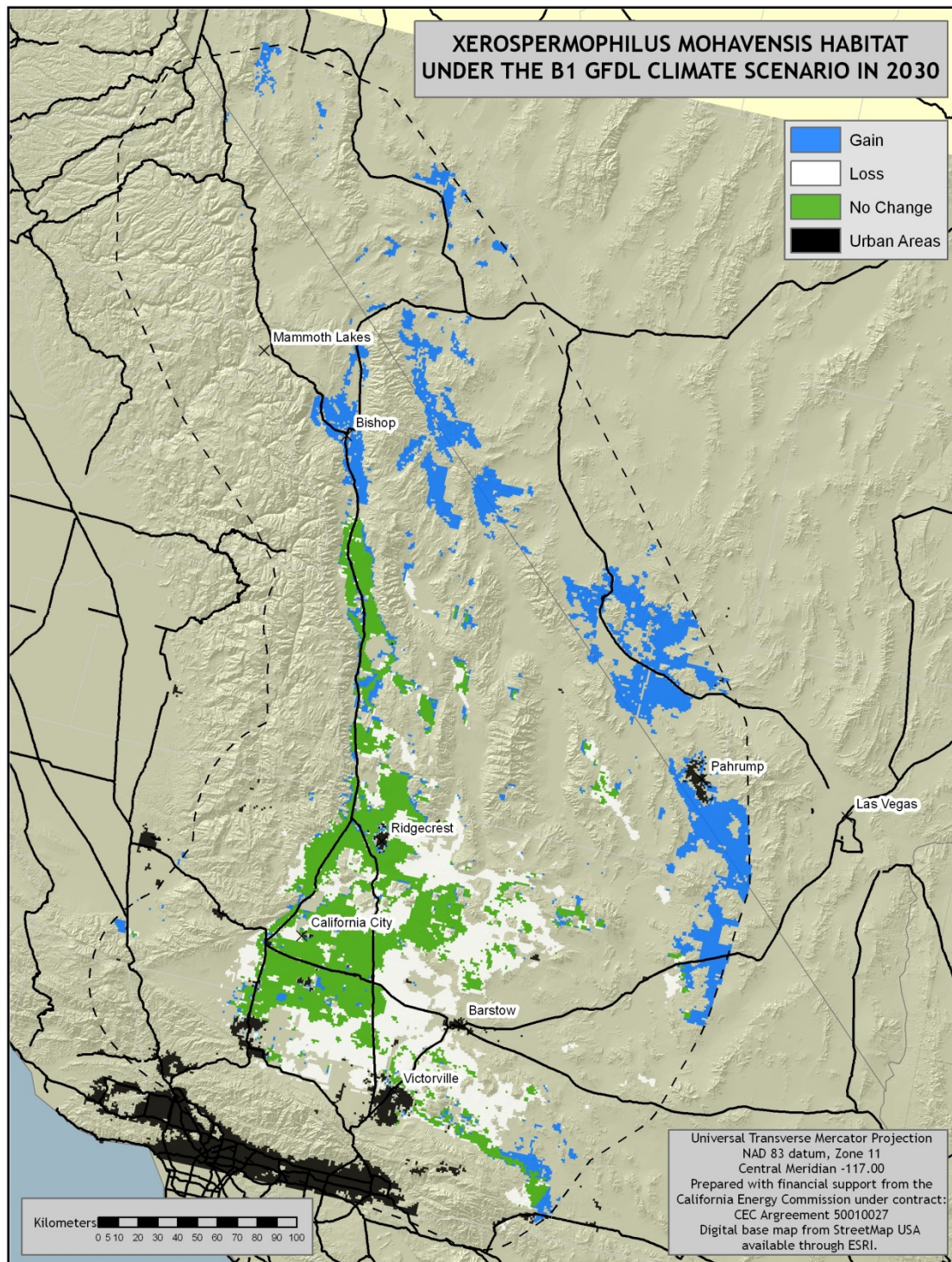
Current habitat that is predicted to remain habitat in 2030 is shown (green), while current habitat that is predicted to become unsuitable is shown in white. New habitat is shown in blue. The study area is shown with a dashed line.

Figure 7: Mohave ground squirrel habitat under the GFDL A2 climate scenario in 2080.
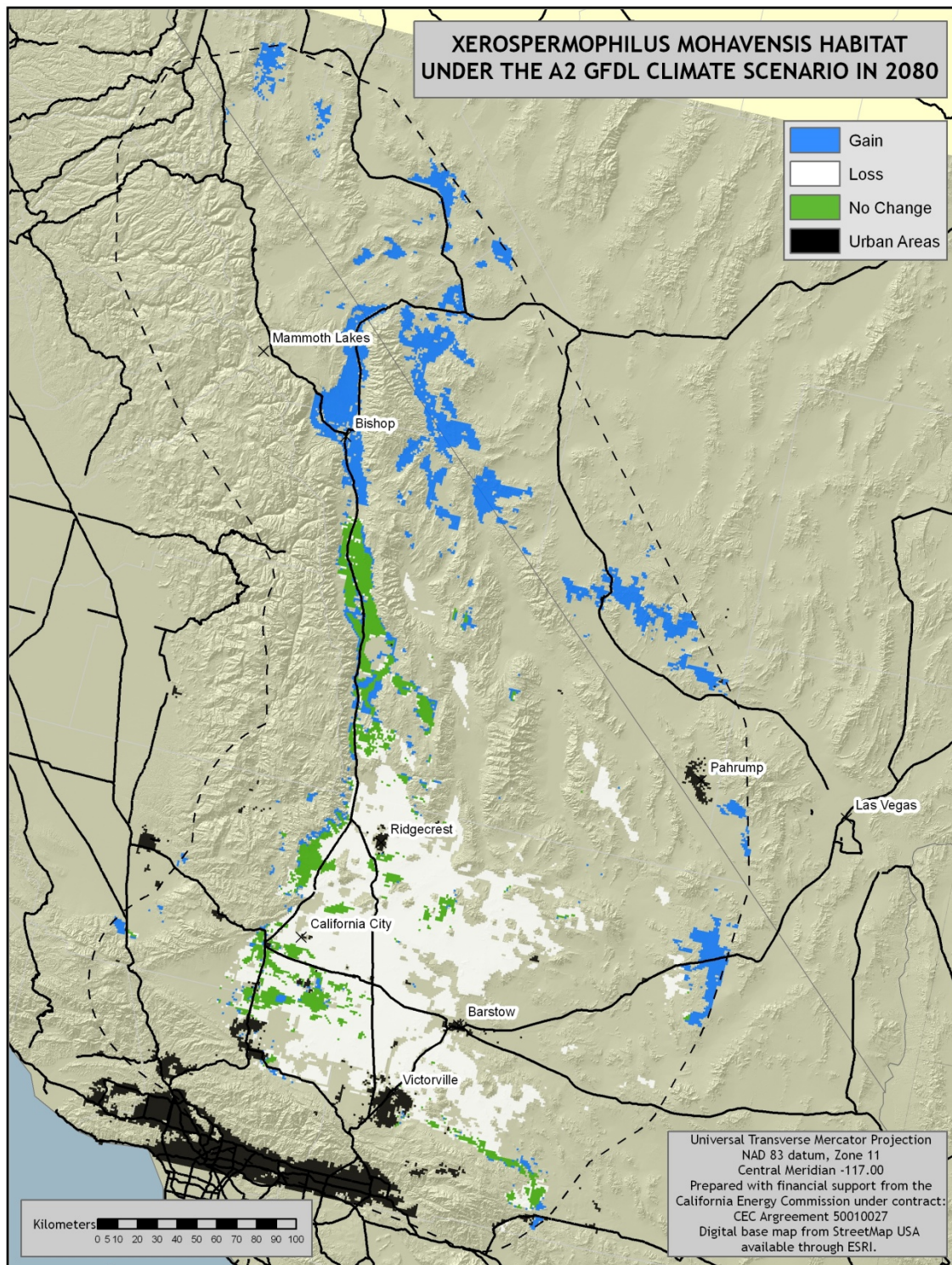
Current habitat that is predicted to remain habitat in 2080 is shown (green), while current habitat that is predicted to become unsuitable is shown in white. New habitat is shown in blue. The study area is shown with a dashed line.

Figure 8: Mohave ground squirrel habitat under the GFDL B1 climate scenario in 2080.
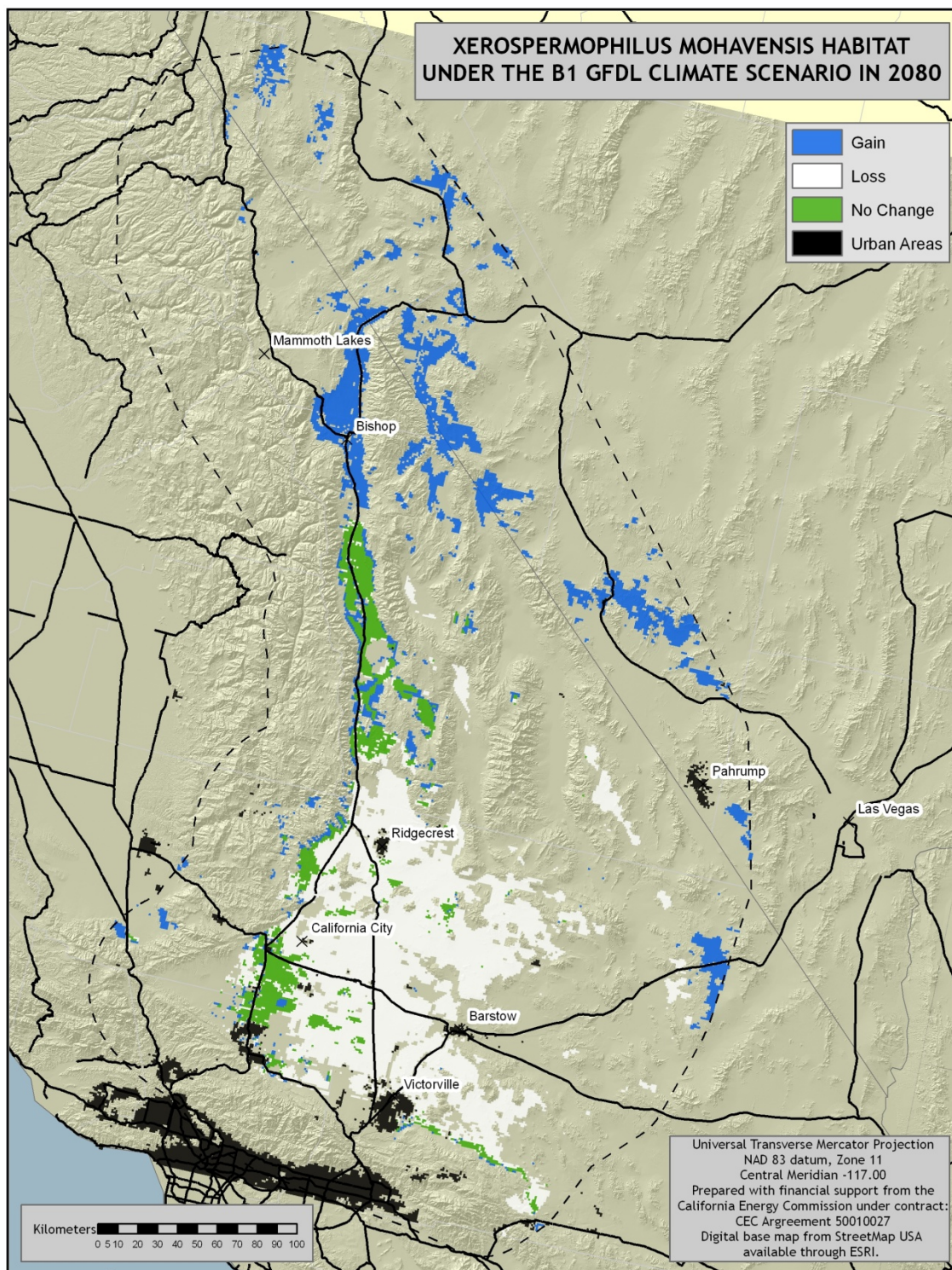
Current habitat that is predicted to remain habitat in 2080 is shown (green), while current habitat that is predicted to become unsuitable is shown in white. New habitat is shown in blue. The study area is shown with a dashed line.

Table 4: Predicted future habitat (loss, gain, and dispersal-limited) under the two GFDL climate scenarios (A2, B1) for two times steps (2030 and 2080) relative to current conditions model.

Year	IPCC Scenario	Total Habitat	Current Habitat Lost		Additional Habitat Gained		Dispersal Limited Habitat	
		km^2			km^2		km^2	
Current	*	16,525	*		*			
2030	A2	14,986	9,422	57.0%	7,876	47.7%	10,774	71.9%
	B1	16,051	8,617	52.1%	8,151	49.3%	11,938	74.4%
2080	A2	8,852	13,863	83.9%	6,172	37.3%	8,539	96.5%
	B1	8,973	13,875	84.0%	6,296	38.1%	8,576	95.6%

Habitat loss was estimated as the amount of current habitat predicted to be unsuitable under future climate scenarios. Habitat gain was estimated as areas currently predicted as unsuitable that may become suitable under future climate scenarios. No consideration for proposed USRED is given.

The majority of co-occurring habitat predicted for 2030 under the GFDL A2 and GFDL B1 climatic scenarios was located north and west of the Victorville area up to Ridgecrest, and north through the Owens Valley to Bishop, California. Additional habitat patches were also predicted south of Pahrump, Nevada (Figure 9). In contrast, the 2080 scenario predicted far less habitat in California City, CA, where the majority of habitat under the current conditions model is located (Figure 10). Habitat predictions under both the GFDL A2 and GFDL B1 climatic scenarios indicate that the majority of habitat for MGS will be located in the Owens Valley north of Ridgecrest up to Bishop, California.

Figure 9: Mohave ground squirrel habitat under the GFDL A2 (red) and B1 (yellow) climate scenarios with overlap (orange) in 2030.

Figure 10: Mohave ground squirrel habitat under the GFDL A2 (red) and B1 (yellow) climate scenarios with overlap (orange) in 2080.
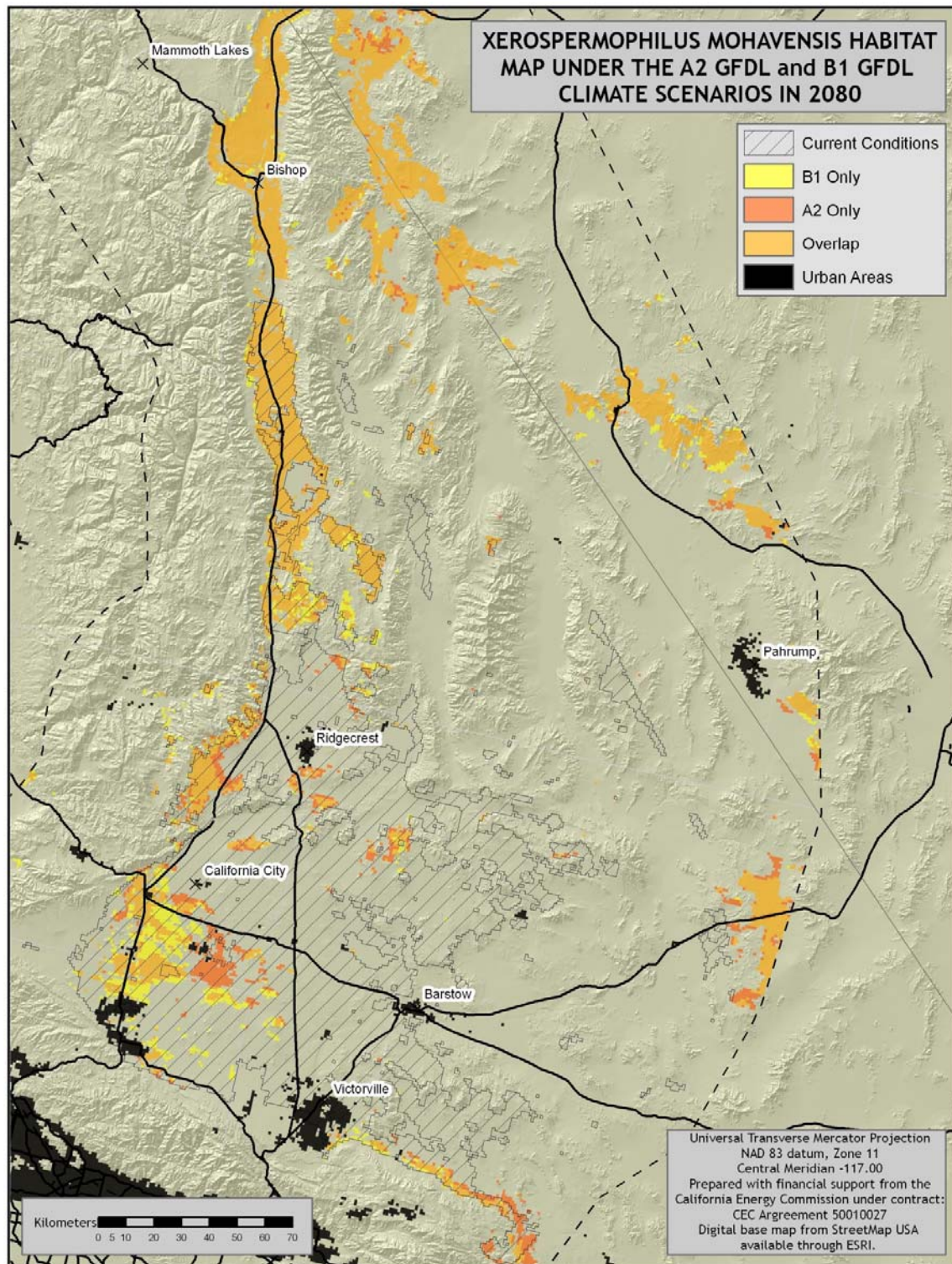
Differences between predicted of habitat under the GFDL A2 and GFDL B1 climatic scenarios were greater in 2030 than 2080, with 1,065 km^2 more habitat under the B1 scenario than under the GFDL A2 climatic scenario in 2030, but only 121 km^2 more by 2080. Overlap between the two habitat predictions was considerable, with 12,558 km^2 of habitat common to GFDL A2 and GFDL B1 predictions in 2030 (Figure 9), and 7,507 km^2 in common by 2080 (Figure 10). In 2030, substantial areas of overlap also occur to the south of California City, CA, and to the west of US Highway 95, north and west of Las Vegas, NV (Figure 9). Far less overlap was predicted in 2080 (Figure 10), and the majority of co-occurring habitat was located in the Owens Valley along US Highway 395, north of Ridgecrest CA, and south of US Highway 6 near Bishop, CA. That area is also consistent with areas of predicted habitat for 2030.

3.3.2 Dispersal-Limited Habitat

Simulating dispersal limitations resulted in 71.9 percent (10,774 km^2) and 74 percent (11,938 km^2) of the potential habitat in 2030 that would be available to MGS under the GFDL A2 and GFDL B1 climatic scenarios, respectively, assuming a dispersal rate of 3 km per year (Table 4; Figures 11 & 12). By 2080 individuals would have had more time to disperse, and as a result, 96.5 percent (8,539 km^2) and 95.6 percent (8,576 km^2) of potential habitat would be available under the two climatic scenarios (Table 4; Figures 13 & 14).

Figure 11: Mohave ground squirrel dispersal limited habitat (blue) and unavailable habitat (red) under the GFDL A2 climate scenarios in 2030.
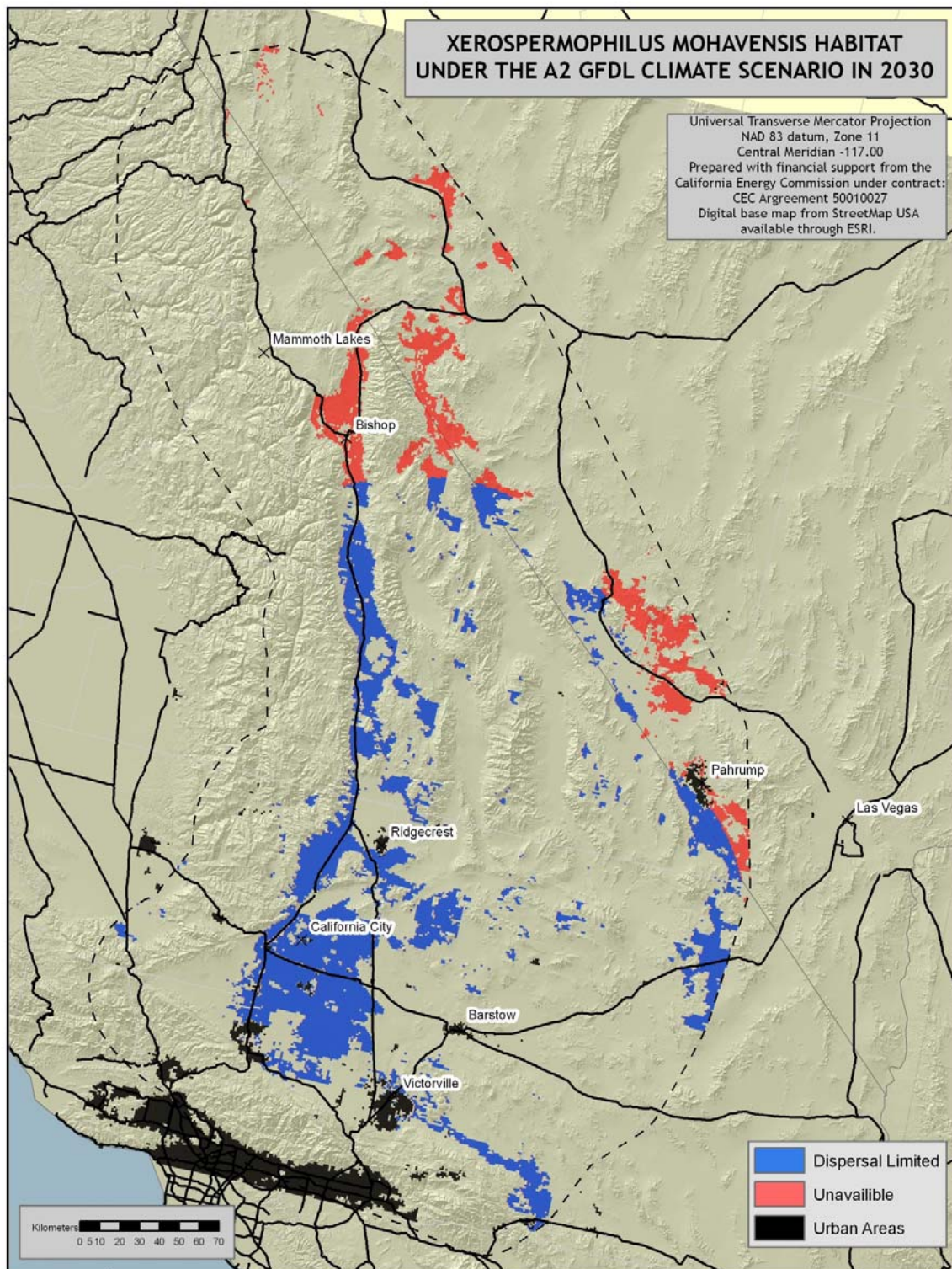
Figure 12: Mohave ground squirrel dispersal limited habitat (blue) and unavailable habitat (red) under the GFDL B1 climate scenarios in 2030.

XEROSPERMOPHILUS MOHAVENSIS HABITAT
UNDER THE B1 GFDL CLIMATE SCENARIO IN 2030

Universal Transverse Mercator Projection
NAD 83 datum, Zone 11
Central Meridian -117.00
Prepared with financial support from the
California Energy Commission under contract:
CEC Argreement 50010027
Digital base map from StreetMap USA
available through ESRI.

Mammoth Lakes

Bishop

Pahrump

Las Vegas

Ridgecrest

California City

Barstow

Victorville

Dispersal Limited
Unavaililble
Urban Areas

Kilometers
0 5 10 20 30 40 50 60 70

Figure 13: Mohave ground squirrel dispersal limited habitat (blue) and unavailable habitat (red) under the GFDL A2 climate scenarios in 2080.
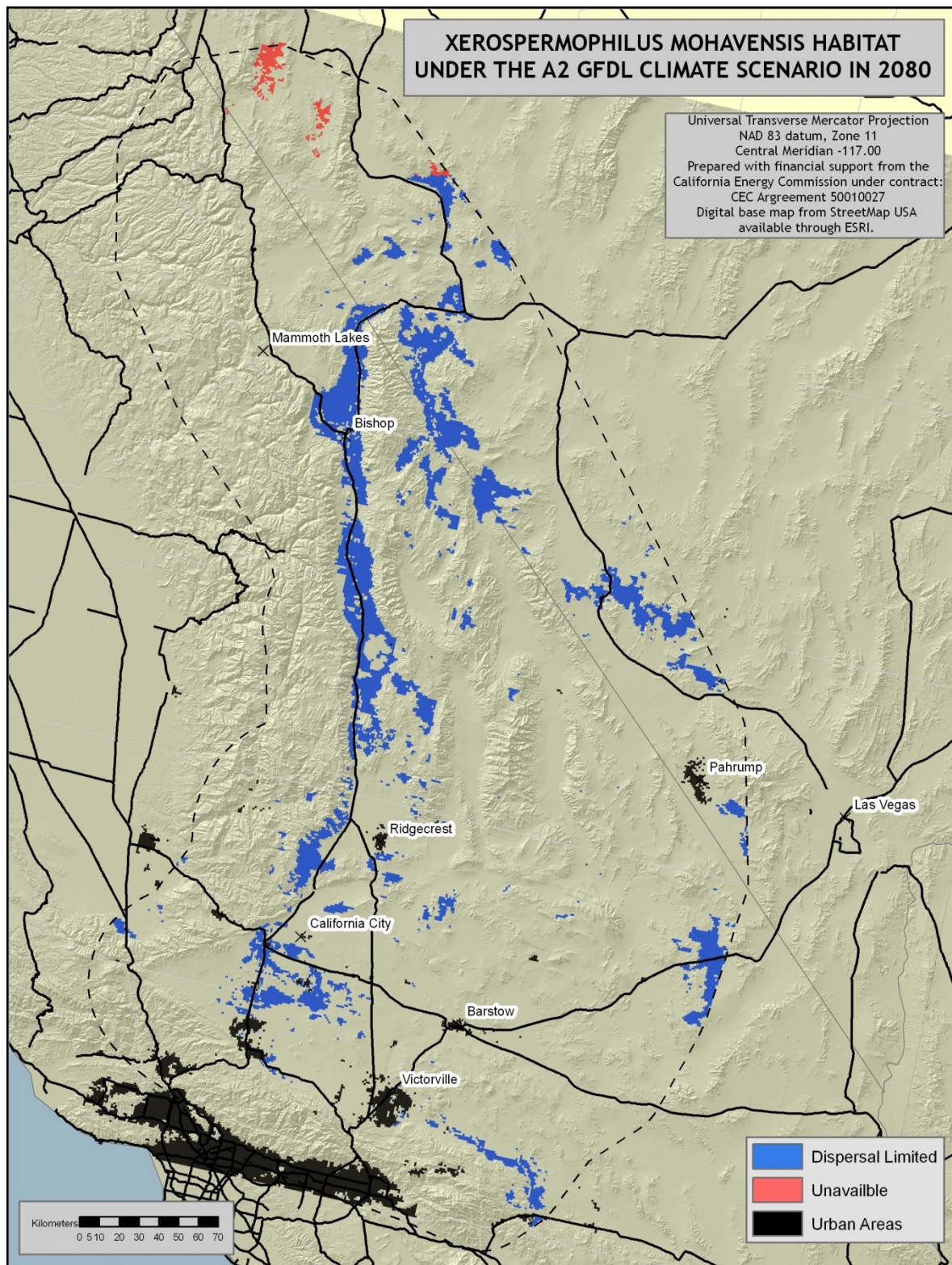
Figure 14: Mohave ground squirrel dispersal limited habitat (blue) and unavailable habitat (red) under the GFDL B1 climate scenarios in 2080.
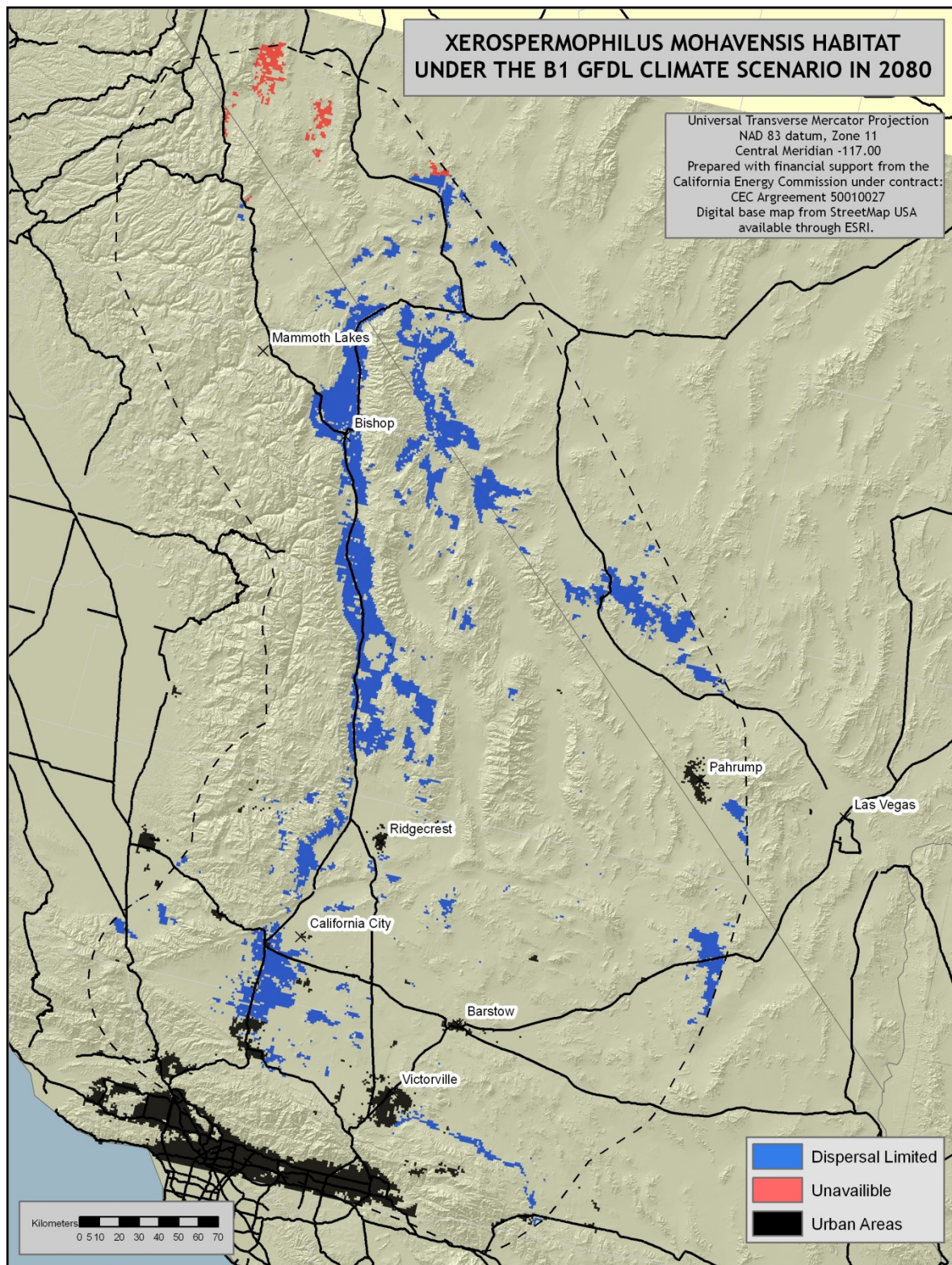
3.3.3 USRED

Although the footprint for USRED that was used in this analysis did not vary through time, the total area and configuration of squirrel habitat varied with each climate change scenario, and each time period resulting in different amounts of impact by USRED. By 2030, the development of USRED will impact an additional 615 km^2 and 641 km^2 of current habitat for the GFDL A2 and GFDL B1 climatic scenarios, respectively (Table 5, Figures 15 & 16). By 2080, the additional habitat impacted by USRED will only be 290 km^2 and 222 km^2 (Table 5), due primarily to the change in geographic distribution of habitat under the two climatic scenarios, respectively. The average habitat suitability score was higher in areas with proposed USRED by 0.052 and 0.057, than the rest of the study area for the GFDL A2 and GFDL B1 climatic scenarios in 2030, respectively. By 2080, the average habitat suitability values were only marginally higher in areas with proposed USRED, with a 0.021 and 0.017 increase for the GFDL A2 and GFDL B1 climatic scenarios, respectively. While higher average suitability scores suggest that areas proposed for USRED have higher suitability habitat than that found across the region, these differences are relatively small compared to the entire range of suitability values (0 ~ 1) predicted in the study area.

Table 5: Predicted future habitat (loss, gain) with proposed USRED under the 2 IPCC emissions scenarios (A2, B1) for 2 times steps (2030 and 2080).

Year	IPCC Scenario	Total Habitat	Current Habitat Lost		Additional Habitat Gained	
		km^2			km^2	
Current	*	16,525	*		*	
2030	A2	13,892	10,037	60.7%	7,439	45.0%
	B1	14,836	9,258	56.0%	7,634	46.2%
2080	A2	8,245	14,153	85.6%	5,929	35.9%
	B1	8,443	14,097	85.3%	6,070	36.7%

Habitat loss was estimated as the amount of current habitat predicted to be unsuitable under future climate scenarios. Habitat gain was estimated as areas currently predicted as unsuitable that may become suitable under future climate scenarios.

Figure 15: Mohave ground squirrel habitat under the GFDL A2 (red) and B1 (yellow) climate scenarios with overlap (orange) in 2030.
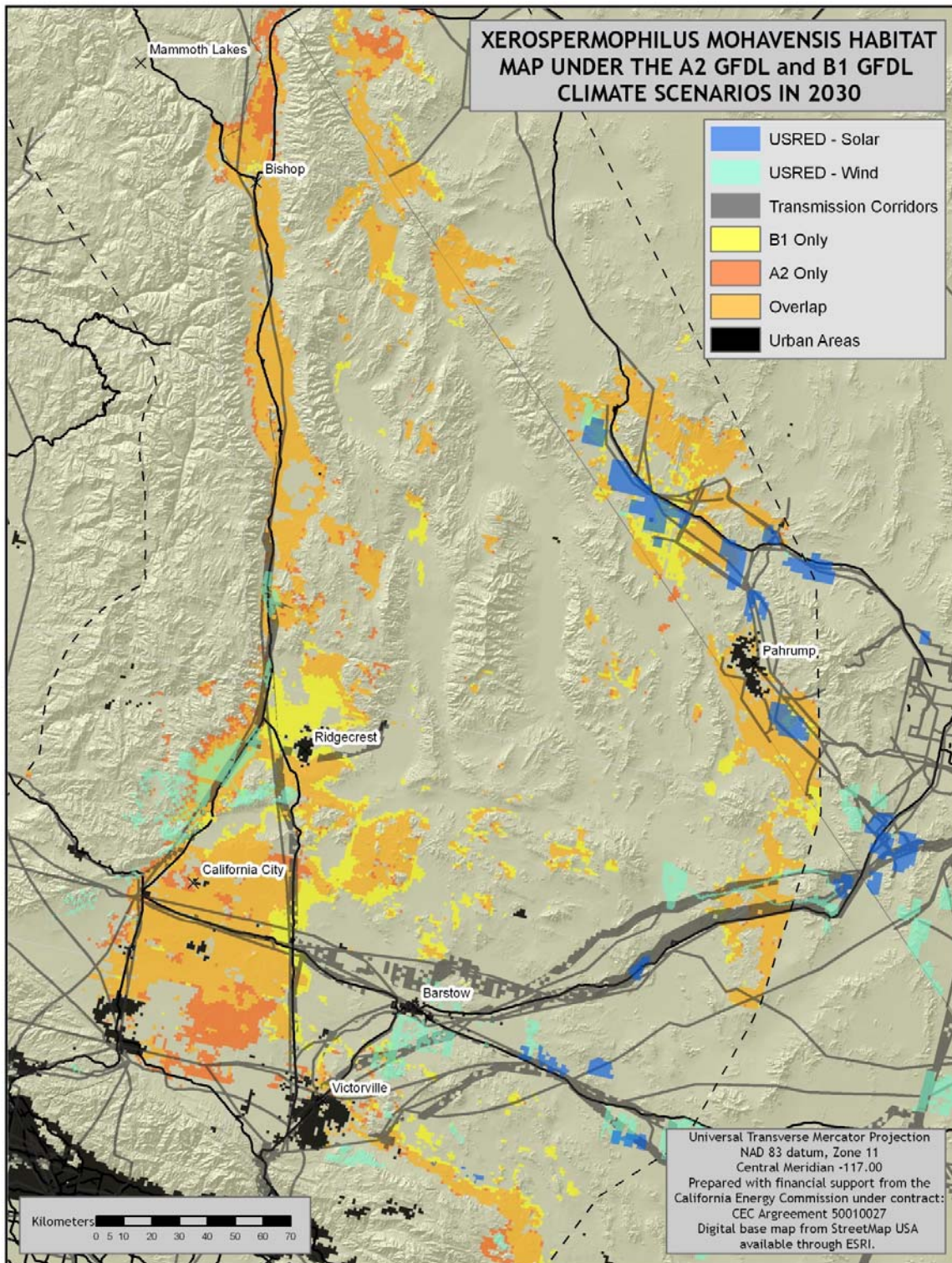
Solar (dark blue) and wind (light blue) USRED is shown along with transmission corridors (grey).

Figure 16: Mohave ground squirrel habitat under the GFDL A2 (red) and B1 (yellow) climate scenarios with overlap (orange) in 2080.
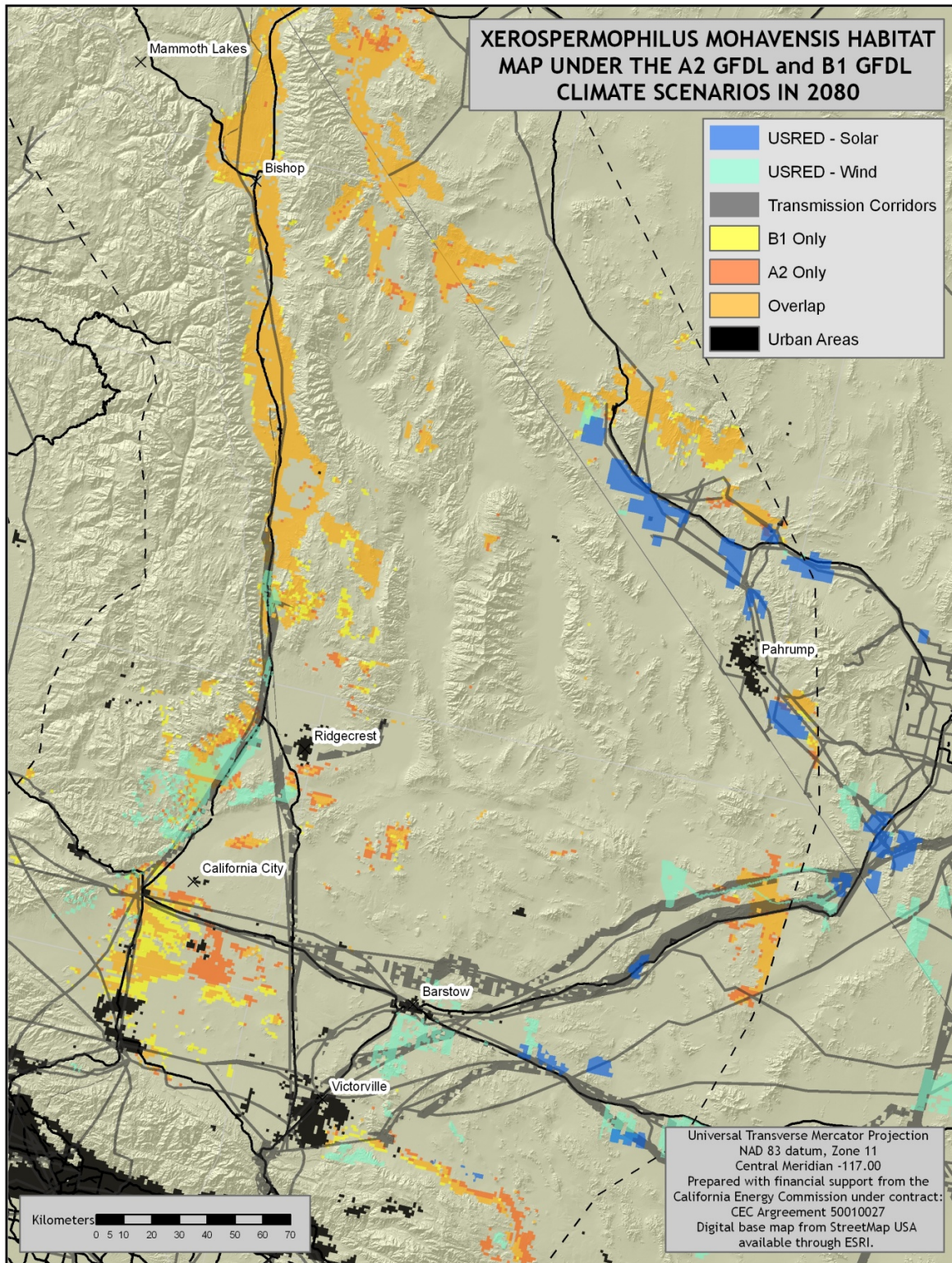
Solar (dark blue) and wind (light blue) USRED is shown along with transmission corridors (grey).

Areas of co-occurring habitat for both of the climatic scenarios that overlapped with proposed wind USRED were found west and south of Ridgecrest, CA, in 2030 (Figure 17) and 2080 (Figure 18). While the amount of overlap was smaller in 2080, this area was also predicted as habitat under the current conditions model. In contrast, the largest areas of overlap between solar USRED and predicted future MGS habitat are not predicted as habitat in the current conditions model. These areas are located north and south of Pahrump, NV in 2030 (Figure 19), but are not predicted to be habitat in 2080 (Figure 20).

Figure 17: Mohave ground squirrel habitat under the GFDL A2 (red) and B1 (yellow) climate scenarios with overlap (orange) in 2030.
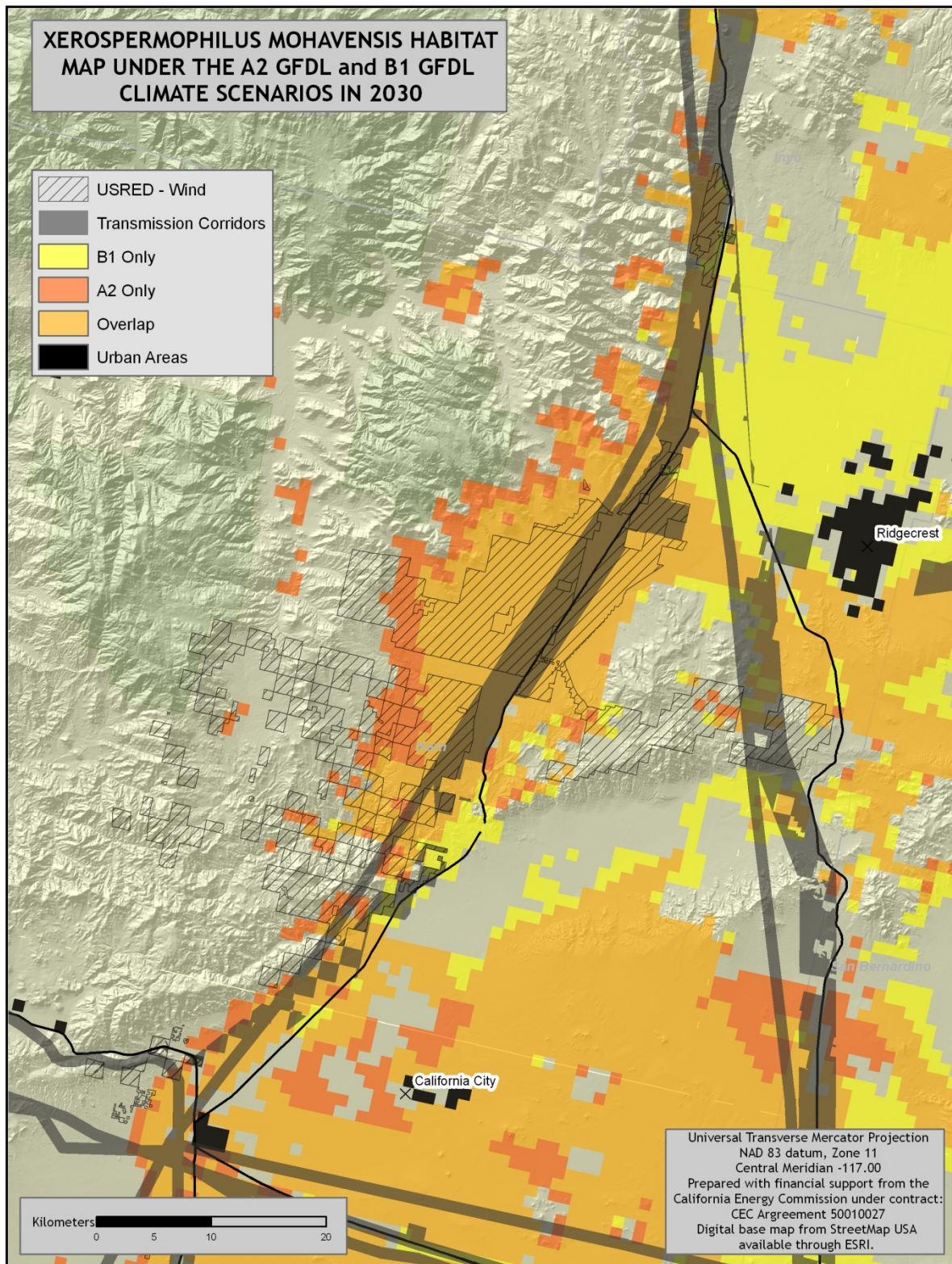
Wind (hashed) USRED is shown along with transmission corridors (grey).

Figure 18: Mohave ground squirrel habitat under the GFDL A2 (red) and B1 (yellow) climate scenarios with overlap (orange) in 2080.
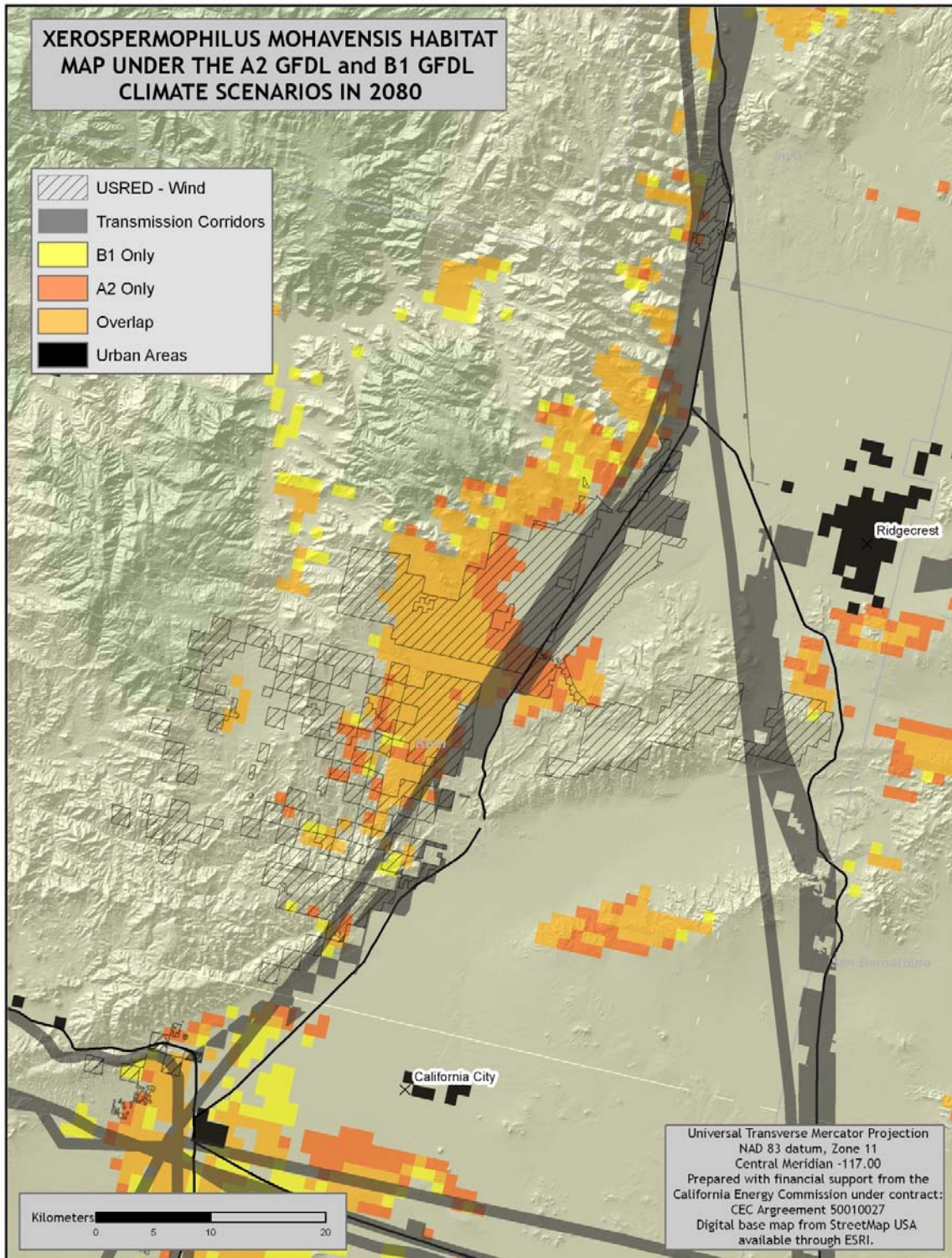
Wind (hashed) USRED is shown along with transmission corridors (grey).

Figure 19: Mohave ground squirrel habitat under the GFDL A2 (red) and B1 (yellow) climate scenarios with overlap (orange) in 2080.
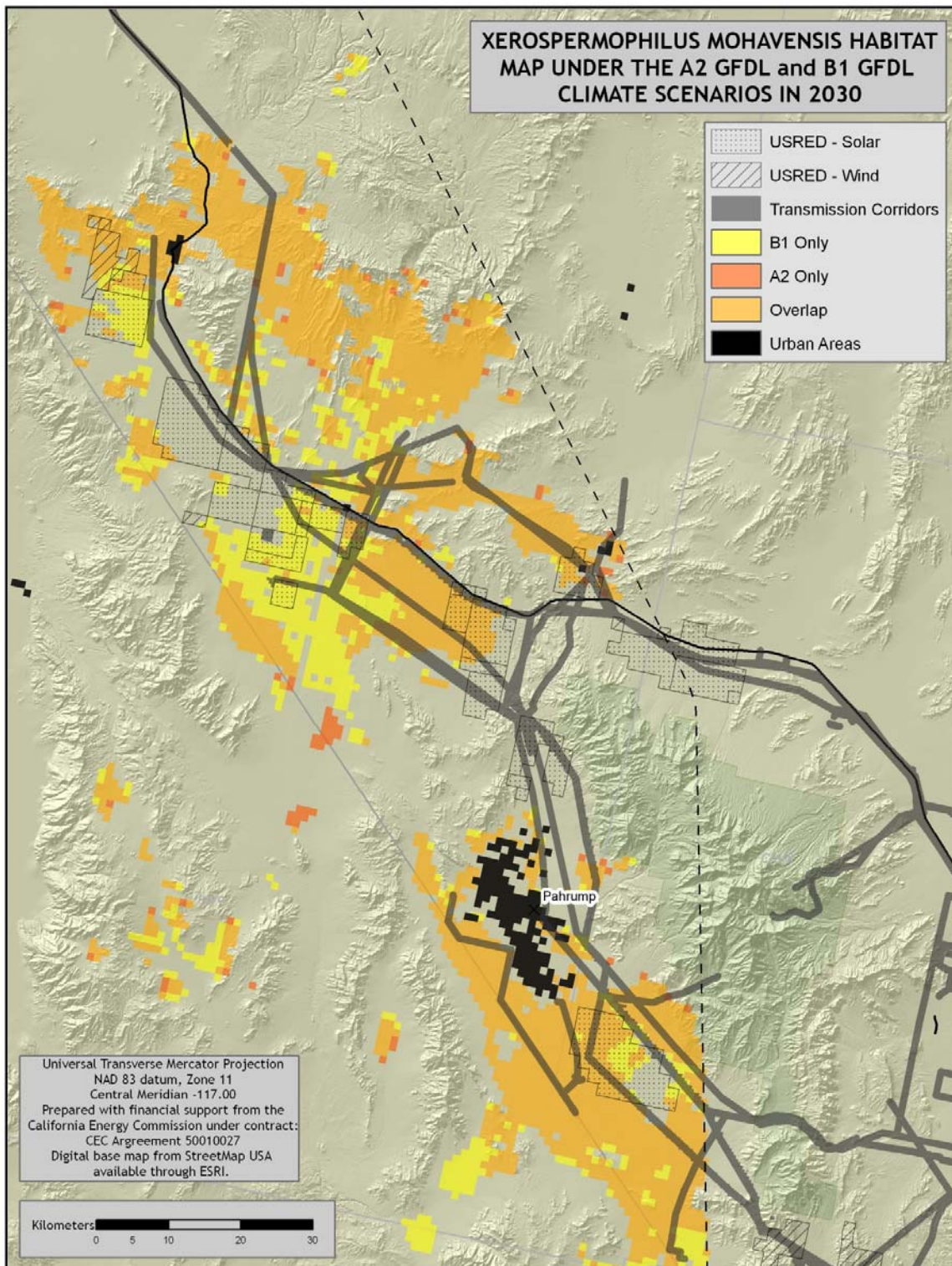
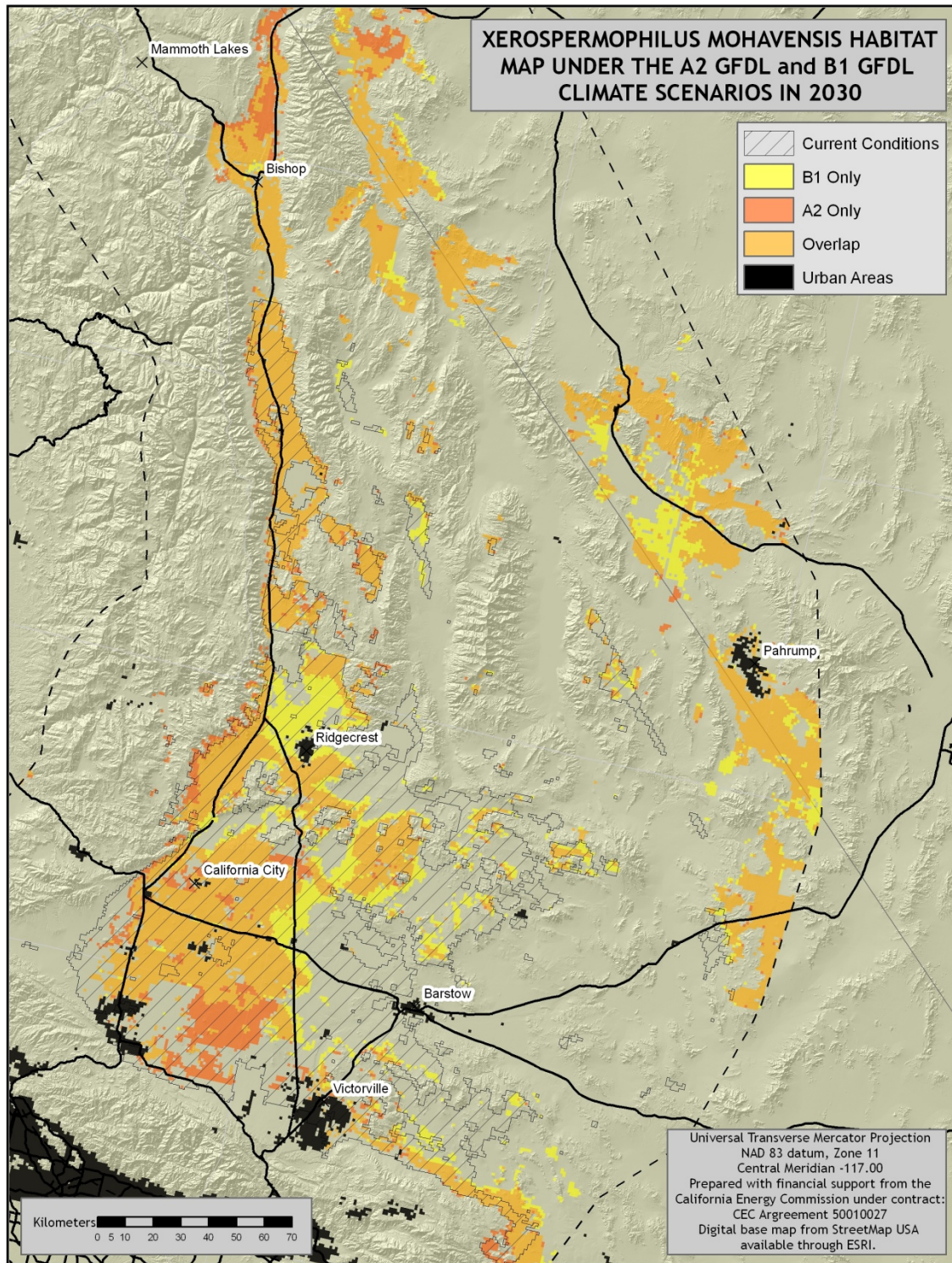Solar (dotted) USRED is shown along with transmission corridors (grey).

Figure 20: Mohave ground squirrel habitat under the GFDL A2 (red) and B1 (yellow) climate scenarios with overlap (orange) in 2080.
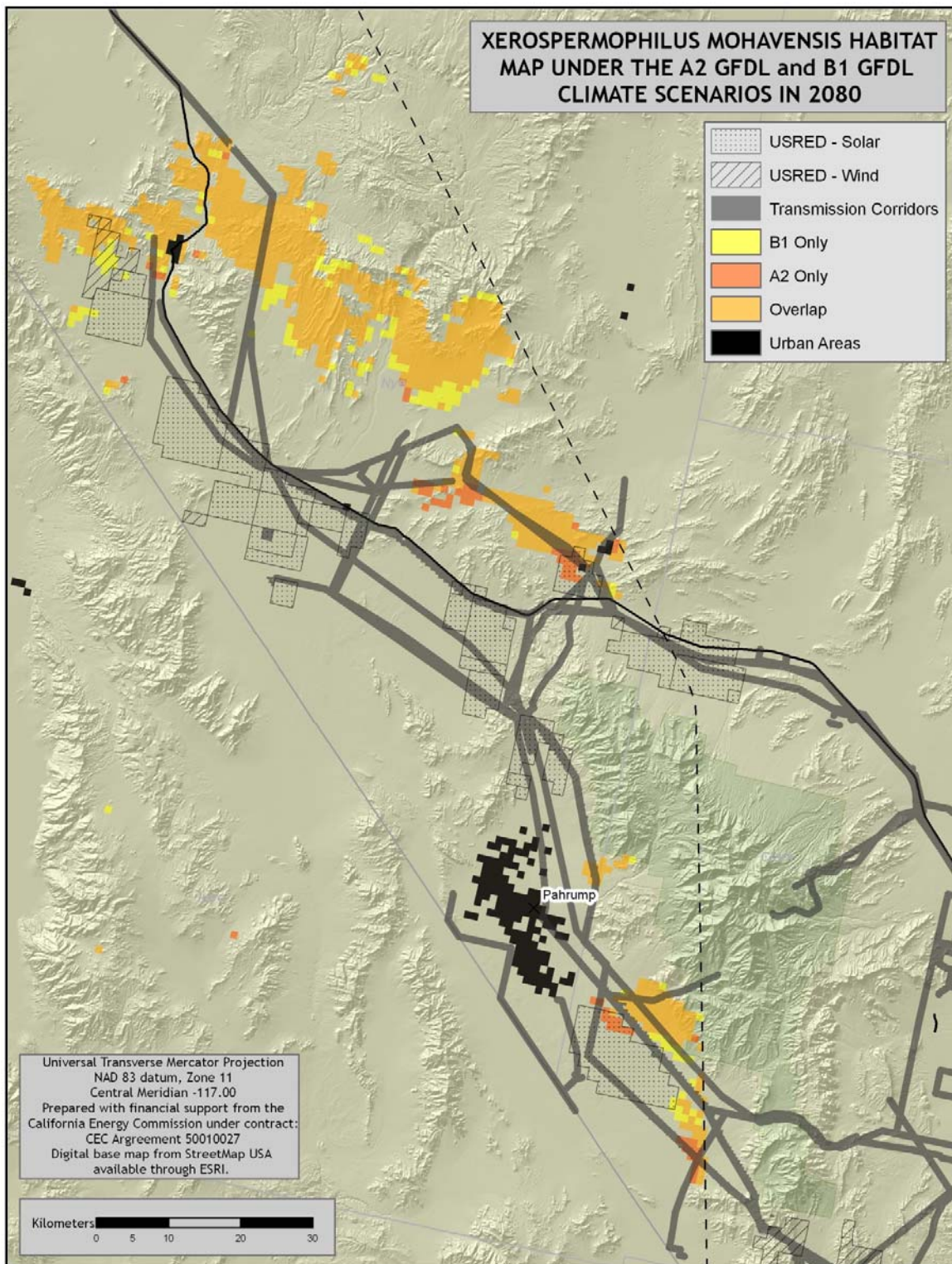
Solar (dotted) USRED is shown along with transmission corridors (grey).

3.4 Discussion

Under the most pessimistic climatic scenario (GFDL A2), current habitat for MGS may be reduced by 84 percent by the year 2080, with further habitat losses of up to 2 percent if currently proposed USRED facilities are constructed. While these predicted losses are over 60 years in the future, predictions for more immediate timescales also resulted in precipitous reductions, with nearly 57 percent loss of current habitat predicted by 2030. These drastic losses of current habitat may be mitigated by additional habitat in the future caused by changing climate. These new areas of potential habitat (up to 8,151 km^2 by 2030; Table 4) may have the characteristics needed to provide suitable habitat for MGS, but due to dispersal limitations, may be unavailable for individuals to occupy. Similar (though less severe) losses were predicted under the GFDL B2 climatic scenario, suggesting that future changes in climate may have strong negative effects on the current distribution of MGS.

Changes expected as a result of the GFDL A2 and GFDL B1 climate scenarios include broad changes to the distribution (Salazar *et al.* 2007, Thomas *et al.* 2008), function (Del Grosso *et al.* 2008), and composition (Lemoine *et al.* 2007, Phillips *et al.* 2008) of ecosystems throughout the globe (see Campbell *et al.* 2009 for review). Responses of species to climate change will likely include shifts in the timing of biological events such as leafing, flowering, and fruiting dates (Gazanfar 1997, Elser and Rundel 1999), hibernation (Lane *et al.* 2011, 2012), migration (Miller-Rushing *et al.* 2008), and mating (Gaston *et al.* 2005, Bronson 2009). These changes to some of the fundamental biological processes of species suggest that climate change may lead to the disruption of community functions, and ultimately, species extinctions at a global scale (Williams *et al.* 2007). Although the probability of extinction for MGS is unknown under either of the climatic scenarios explored here (see Chapters 4 & 5), it is apparent that the loss of current habitat, and its importance for maintaining genetic diversity (see Chapter 4) and connectivity (see Chapter 5) will drastically impact the future of this species.

Recent work has shown that the ranges of small mammals at high elevations in California, USA, decreased within the last century, likely due to climate change (Moritz *et al.* 2008). Others have predicted that the distributions of many rodent species in Texas, USA, will decrease to 60 percent of their current distributions under some GCM predictions (Cameron and Scheel 2001). Although many such changes occurred during previous climate changes (Betancourt *et al.* 1990), the landscape scale changes wrought by recent human development may further hinder some species' abilities to adapt to the rapidly changing landscape (Schloss *et al.* 2012), resulting in range contractions and population declines.

When dispersal limitations were considered for MGS, nearly 30 percent of potential habitat in 2030 may be unavailable. The representation of dispersal-limited habitat for MGS described here is likely an oversimplification because many important fundamental life history traits are unknown for MGS, and the authors did not include estimates of dispersal costs or barriers to movement. Where possible, such considerations are evaluated in Chapter 5. Much of the potential habitat that may become available under future climates is separated from current habitat by expanses of unsuitable habitat, including barriers to movement such as mountain ranges (Figures 9 & 10). Although potential habitat may become available under future

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climates, it is not clear whether those areas will be within reach for individuals because barriers to movement may preclude invasion of MGS from new habitats under various climate scenarios (Rodda *et al.* 2011). Furthermore, should they reach new areas of potential habitat predicted by this model, the question of whether or not sufficient resources exist to support them still remains.

By 2080, a large portion of potential habitat for MGS is predicted to be located in the Owens Valley, along US Highway 395. This relatively narrow valley is flanked by the Sierra Nevada, White Mountains, and stretches north from Owens Lake, CA, up through Bishop, CA. No known efforts to sample for MGS have been made there, though the northern most observation of MGS is on the southeastern edge of the Owens Lake, suggesting that this valley may not be too dissimilar from current habitat. Overlap between predictions of MGS habitat under the two climate scenarios was substantial in the Owens Valley at both time scales (Figures 9 & 10), also suggesting that future habitat may be located there. Additional areas to the east of Bishop, CA, on the east side of the White Mountains, are also predicted to be habitat under the two GFDL A2 and GFDL B1 climatic scenarios in 2030 and 2080 (Figures 9 & 10).

Losses of current habitat due to the combination of climate change and proposed USRED was predicted to be over 60.7 percent by 2030 under the GFDL A2 climatic scenario by 2030, but in the absence of USRED, habitat loss was predicted to be 57.0 percent. Current habitat lost due to USRED was marginal relative to habitat lost due to changes in climate, though the proposed USRED equates to nearly 616 km^2 of additional habitat that may be lost by 2030. By 2080, proposed USRED may represent an additional 290 km^2 of habitat that may be lost in addition to the 13,863 km^2 of habitat that may be lost due to changes in climate under the GFDL A2 climatic scenario. Similar losses were predicted under the GFDL B1 climatic scenario, suggesting that while the two climatic scenarios are different in their forecasts of future climate, their predictions of MGS habitat were not dissimilar in light of proposed USRED. Although only USRED on BLM lands were considered, renewable energy projects on private lands may cause additional loss of MGS habitat. Similarly, the spatial footprints of the USRED (described in Chapter 2) used for these analyses were accurate as of October 2010, and represent a snapshot of proposed USRED at that time. Due to continuous changes in applications and permits, the best available data are continually replaced with new plans for USRED.

One area of conservation concern that will be affected by proposed wind energy is located west and south of Ridgecrest, CA (Figures 17 & 18). This area was predicted as potential habitat under both climatic scenarios, suggesting that it will remain suitable under a range of climate forecasts. This area also serves as an important corridor for gene flow among populations in the current distribution of MGS (see Chapters 4 & 5 for review), and currently contains one of three distinct genetic groups within the species (Bell and Matocq 2011). Under future climate regimes, this area may also serve as an important corridor of habitat to facilitate movement of individuals from areas that may become unsuitable. It was assumed that the impacts of solar energy projects may be greater to MGS than wind energy projects, and this is reflected in the selection of scale factors for USRED (see Chapter 2 for discussion). This area is slated for wind energy development only. Rabin *et al*. (2006) suggest that increased alert vocalizations and anti-predator vigilance behavior may occur in California ground squirrels (*Otospermophilus beecheyi*)

due to the additional noise generated by the blades of the wind turbine props. However, little is known about the cumulative impacts these USRED facilities will have on the status of small mammal populations.

Although not currently Mohave ground squirrel habitat, a large area north and south of Pahrump, NV, was also identified for conservation concern because it is predicted to be habitat by 2030 under both climate scenarios and may be affected by solar USRED (Figure 19). However, by 2080, the amount of potential habitat in this area will be substantially reduced, such that conflict between USRED and suitable habitat will be minimal (Figure 20). Furthermore, this area is not within the current predicted distribution of MGS, and is likely unreachable by individuals due to barriers to movement (both natural and man-made) without intervention such as assisted migration (McLachlan *et al*. 2007). Therefore, it is surmised that while the direct effects of solar USRED are likely more detrimental to MGS populations than wind USRED (see *scale factors* in Methods and Chapter 2 for general discussion), wind energy USRED presents the greater potential for detrimental effects on predicted MGS habitat under the two climatic scenarios.

Climate change issues and research have been at the forefront of public interest and scientific investigations in recent years. The need for new tools to relate species responses to changes in climate has caused scientists to modify existing tools used for modeling habitat to incorporate forecasts of climate change into future predictions of habitat availability. However, while habitat models used in this manner provide quantitative predictions of habitat in a changing world, they are not without error, and should be interpreted as predictions with assumptions and inherent error. Few methods exist to represent all of the uncertainty inherent in the predictions of future habitat because of the many sources of error contained in each of the GCMs (Tebaldi *et al*. 2005, Collins *et al*. 2011), emissions scenarios (IPCC 2001), downscaled climate variables (Flint and Flint 2012) and habitat models (Rocchini *et al*. 2011). The predictions of MGS habitat are based on the best available knowledge and data, but will undoubtedly be improved upon by future modeling, because scientists continue to improve and refine global climate models and emissions scenarios, and continue to refine our understanding of species' habitat requirements and inter-species interactions. Reduced uncertainty and improved utility will help future efforts to be more precise in deriving estimates of future habitat suitability.

Resource managers charged with preserving biodiversity while managing for multiple uses of public lands face increasing demands and pressures as development continues in the desert southwest (Wood *et al*. 2012). The models predicted substantial loss of current habitat by 2080, even under the least extreme of the two climatic scenarios, suggesting that conservation of current habitat for this rare and endemic species is even more critical than previously thought.

CHAPTER 4:
Historic and ongoing processes contributing to genetic diversity and divergence in the Mohave ground squirrel (*Xerospermophilus mohavensis*)

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4.1 Introduction

Identifying the current spatial distribution of genetic variation within a species is critical not only to inferring historic and ongoing evolutionary processes that have generated and maintained genetic diversity. It is also central to establishing land use practices that may contribute to sustaining the evolutionary potential of species. Here, the current state of knowledge concerning the geographic distribution of genetic diversity in the Mohave ground squirrel (MGS, *Xerospermophilus mohavensis*) is reviewed. The information (some already in the published literature) establishes both historic and ongoing factors that contribute to patterns of genetic variation within the species. Beginning with a broad geographic and deep temporal perspective the focus is progressively narrowed to regional patterns of variation within the species, and ends with the most fine-scale view of factors contributing to the distribution of diversity within a particularly well-sampled population. Genetic information is linked to the habitat suitability and landscape connectivity data presented in earlier chapters of this report by examining if patterns of genetic distance are correlated with habitat-based distances among localities. Finally, a simulation approach is used to begin an examination how various climate change scenarios might impact patterns of genetic diversity in this species. Throughout, efforts are made to maximize the use of information currently in hand, while identifying critical knowledge gaps and setting priorities for continued research.

4.2 Background

Recent analyses of the phylogeographic history (Bell *et al*. 2009) and regional population genetic structure (Bell and Matocq 2011) of *X. mohavensis* provided information concerning broad-scale patterns of variation in the species throughout its current distribution. Using phylogenetic analysis and molecular dating of mitochondrial cytochrome *b* sequence variation in *X. mohavensis* and *X. tereticaudus*, Bell *et al*. (2009) showed that the two species likely diverged from one another *c*. 1.6 million years ago. Coarse reconstructions of Mojave-region paleolandscapes suggest that divergence between the two species may have been caused by vicariance associated with the uplift of the Transverse Range and subsequent isolation of the Antelope and Phelan Peak basins (Bell *et al*. 2009). Genetic patterns of relative population stability characterize the southern portion of the MGS range while the northern-most region (Olancha, Coso Basin, and Cactus Peak) shows a signature of expansion *c*. 11.7 thousand years ago (Bell *et al*. 2009). These patterns of stability and expansion suggest that even through pluvial cycles of the late Pleistocene and continued riverine dynamics of the Holocene, portions of the southern end of

the distribution were likely continuously occupied, while the northern reaches of the range may have more recently been colonized or re-colonized.

Set within the broad geographic and temporal framework established by Bell *et al*. (2009), Bell and Matocq (2011) used rapidly evolving nuclear microsatellite loci to identify regional and inter-population genetic structure within *X. mohavensis.* Based on a Bayesian assignment test approach, they found three regional genetic groups within the range of *X. mohavensis*, largely associated with 1) the northern portion of the range (Olancha, Cactus Peak, Coso Basin); 2) the central portion of the range (Freeman Gulch, El Paso Mountains); and 3) the southern portion of the range encompassing the Desert Tortoise Natural Area (DTNA), east through Fort Irwin (Figures 21 and 22). Although these areas are largely characterized by one of the three genetic groups, gene flow among the groups is evident with many individuals, especially in the Johannesburg and Poison Canyon areas, showing admixed genomes (Figure 22). Bell and Matocq (2011) conclude that patterns of genetic structure within *X. mohavensis* are largely the result of historic vicariant events associated with the Owens River system and subsequent colonization or recolonization of portions of the range, especially to the north and in the vicinity of Johannesburg and Poison Canyon.

Figure 21. Map of Mohave ground squirrel genetic localities and the extent of the historic Owens River system.

Figure 22. Bayesian analysis showing the genomic composition of individuals within sampling localities of *X. mohavensis*.
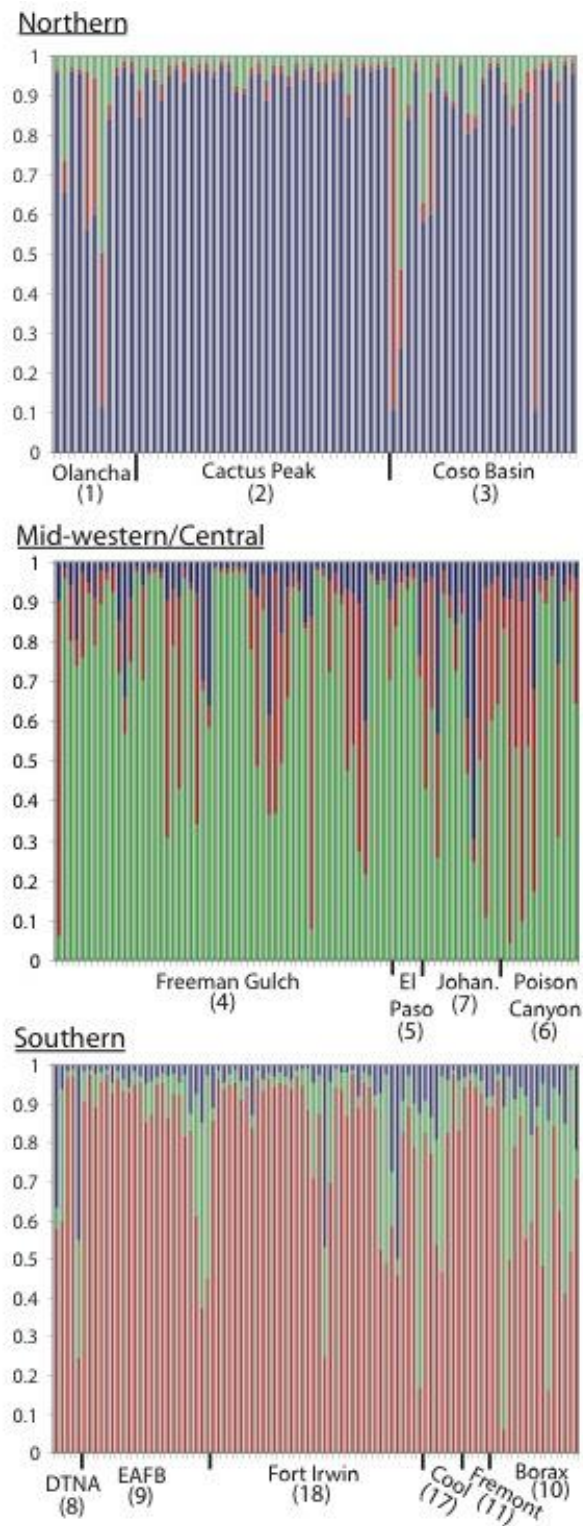
Vertical lines show the genomic composition of individual squirrel. Three primary genetic groups are evident (blue = northern, green = mid-western/central, red = southern) but admixture among the groups is clearly evident. Modified from Bell and Matocq (2011).

Frequency-based estimates (F_{ST}) of genetic subdivision among populations within *X. mohavensis* were low to moderate with the northern populations being the most distinct and more genetic exchange evident between central and southern regions (a pattern also evident from the Bayesian analysis, Figure 22). Comparing genetic distances among localities to straight-line Euclidean distances yielded a significant relationship (P< 0.007) but with only 13 percent of the variation in genetic distance being explained by straight-line geographic distance. The lack of a strong relationship between genetic and geographic distance could indicate that portions of the range have not reached an equilibrium between drift and migration, as would be expected in a species like *X. mohavensis* that has likely come to occupy or reoccupy large portions of its range within Holocene times. It is also possible, and not to the exclusion of non-equilibrium in parts of the range, that genetic distances among populations may better correlate with habitat-based 'distances' between localities rather than straight-line distances. The habitat suitability and landscape connectivity analyses presented in this report (Chapter 5) provide an opportunity to expand earlier analyses and identify further relationships between genetic distances and habitat-based estimates.

As made clear by Bell and Matocq (2011), the distances among currently sampled localities within the range of *X. mohavensis* exceed individual dispersal capabilities and, thus, current estimates of genetic differentiation reflect long-term connectivity across multiple generations. As sampling efforts continue into the future, these large distances (relative to individual dispersal) will be reduced, allowing a refined understanding of the relationship between individual movements, gene flow, and characteristics of the landscape. While such sampling is currently unavailable, it is possible to investigate the most local scale of individual movement and genetic structure within *X. mohavensis*. Using data from the Freeman Gulch area, fine-scale population genetic structure was investigated to gain insight about factors contributing to localized gene flow.

After examining the degree to which genetic distance is correlated with various habitat-based distances and identifying the most local scale at which genetic variation is structured in this species, all data in hand were used to establish a simulation of how the species may respond to future climate change. Taken together, these analyses present the current best estimate of genetic variation within *X. mohavensis* and the initial exploration of how this variation may change in light of different climate change scenarios.

4.3 Methods

4.3.1 Underlying correlates of genetic distance within *X. mohavensis*

Using the microsatellite dataset of Bell and Matocq (2011) with slight modifications of adding newly available individuals to certain populations, the researchers estimated population pairwise linearized F_{ST} (Rousset 1997) using GENALEX (version 6.2; Peakall and Smouse 2006). The geographic locations of population centroids are shown in Figure 21. As an alternative to straight-line Euclidean distance two measures of habitat-based distances were used. Both

habitat-based approaches first require a resistance map, which was calculated by inverting the habitat model (Chapter 2, this report). Given the short distance of MGS dispersal relative to the cell size used for the habitat model it was assumed that movement between populations is inversely and linearly related to habitat suitability (i.e., MGS are less likely to move through poor compared to higher quality habitat). Both cost-weighted distance (Adriaensen *et al*. 2003) and cumulative resistance (McRae 2006) were used as measures of habitat-based distance. Cost-weighted distance uses Dijkstra's algorithm to determine an optimal least-cost route between populations and sums the resistance values for each cell along the single optimal route. In contrast, cumulative resistance is based on circuit theory and does not assume a single optimal route, but rather integrates numerous potential routes into one overall measure of cumulative resistance. UNICOR software was used to calculate cost-weighted distance among populations (Landguth and Cushman 2010) and Circuitscape to calculate cumulative resistance (McRae and Shah 2009) between populations. Finally, in addition to habitat-based resistance of the landscape, the influence of a potential discrete barrier, namely, the course of the Owens River system was also examined.

Typically, in landscape genetics studies, the various measures of habitat-based distance are correlated with one another as well as with Euclidean distance and even with 'barrier distances', those derived from discrete barriers on the current or historic landscape. This poses a problem in that causation may be falsely attributed to the wrong agent (Cushman and Landguth 2010a). In an attempt to overcome this, a partial Mantel's tests was used to determine the significance of each type of distance even after accounting for the effect of other forms of distance (Table 6).

4.3.2   Fine-scale genetic structure: insight from Freeman Gulch

Using methods described in Bell and Matocq (2011), 17-locus microsatellite genotypes for 143 individuals captured in the Freeman Gulch area in 2002-2004 were generated (Figure 23). A spatial genetic autocorrelation analysis (Epperson 2005) was conducted using GENALEX to identify the spatial scale of localized genetic structure (Peakall *et al*. 2003). The geographic location of each individual was set as their first point of capture. The multivariate (*i.e.*, multilocus) approach of Smouse and Peakall (1999) was used to generate an autocorrelation coefficient (*r*), which is similar to Moran's-I and is a measure of genetic similarity between pairs of individuals located within particular distance classes. Distance class bins of 25m, 50m and 100m were used to explore how partitioning individuals into different classes might influence the inferred scale of localized gene flow. Although field trapping was not conducted on a standardized grid, 25 m distances between traps were typical when making efforts to capture adjacent individuals, especially mothers and their pups. As such, most analyses are conducted at 25 m intervals to reflect the nature of the original trapping effort. Confidence intervals (C.I.) to estimate *r* were determined by 999 bootstrap resamplings and C.I. around the null hypothesis of no genetic structure using 999 permutations (random shuffling of individuals among locations). Autocorrelograms were generated in GENALEX to facilitate visual inspection of the data. Finally, patterns of genetic correlations were compared between age and sex classes at multiple distance classes using the *Multiple Dclass* option in GENALEX and estimated confidence

intervals as above. The latter analysis is considered most sensitive to detecting the spatial extent of positive genetic structure (Peakall et al. 2003).

Table 6: Results of the partial Mantel's test for the significance of the relationship between genetic distance and various measures of geographic distance.

Distance Used	Distance Held Constant	R-squared	Right-tailed p value	Significance
Barrier		0.27	0.003	***
Barrier	Eucl	0.32	0.003	***
Barrier	CWD	0.31	0.002	***
Barrier	CR	0.26	0.003	***
Barrier	Eucl, CWD	0.34	0.003	***
Barrier	CWD, CR	0.27	0.002	***
Barrier	Eucl, CWD, CR	0.28	0.002	***
Euclidean		0.15	0.001	***
Euclidean	Bar	0.00	0.423	
Euclidean	Eucl	0.00	0.424	
Euclidean	CR	0.00	0.522	
Euclidean	Bar, CWD	0.02	0.845	
Euclidean	Bar, CR	0.02	0.192	
Euclidean	Bar, Eucl, CR	0.02	0.745	
Cost-weighted		0.17	0.003	***
Cost-weighted	Bar	0.02	0.258	
Cost-weighted	Eucl	0.01	0.718	
Cost-weighted	CR	0.02	0.202	
Cost-weighted	Bar, Eucl	0.06	0.113	
Cost-weighted	Bar, CR	0.01	0.74	
Cost-weighted	Eucl, CR	0.02	0.862	
Cost-weighted	Bar, Eucl, CR	0.00	0.396	
Cumulative Resistance		0.25	0.001	***
Cumulative Resistance	Bar	0.05	0.116	
Cumulative Resistance	Eucl	0.10	0.019	**
Cumulative Resistance	CWD	0.12	0.019	**
Cumulative Resistance	Bar, Eucl	0.07	0.082	*
Cumulative Resistance	Bar, CWD	0.04	0.116	
Cumulative Resistance	Eucl, CWD	0.12	0.007	***
Cumulative Resistance	Bar, Eucl, CWD	0.02	0.213	

Correlation is measured with r-squared values. Bar = presence of a pluvial lake/river barrier, Eucl = Euclidean distance, CWD = Cost-weighted distance, CR = Cumulative Resistance
* = significant at the 0.1 level, ** = significant at the 0.5 level, *** = significant at the 0.01 level

Figure 23. Fine-scale distribution of 143 Mohave ground squirrels (green dots) in Freeman Gulch from 2002-2004.
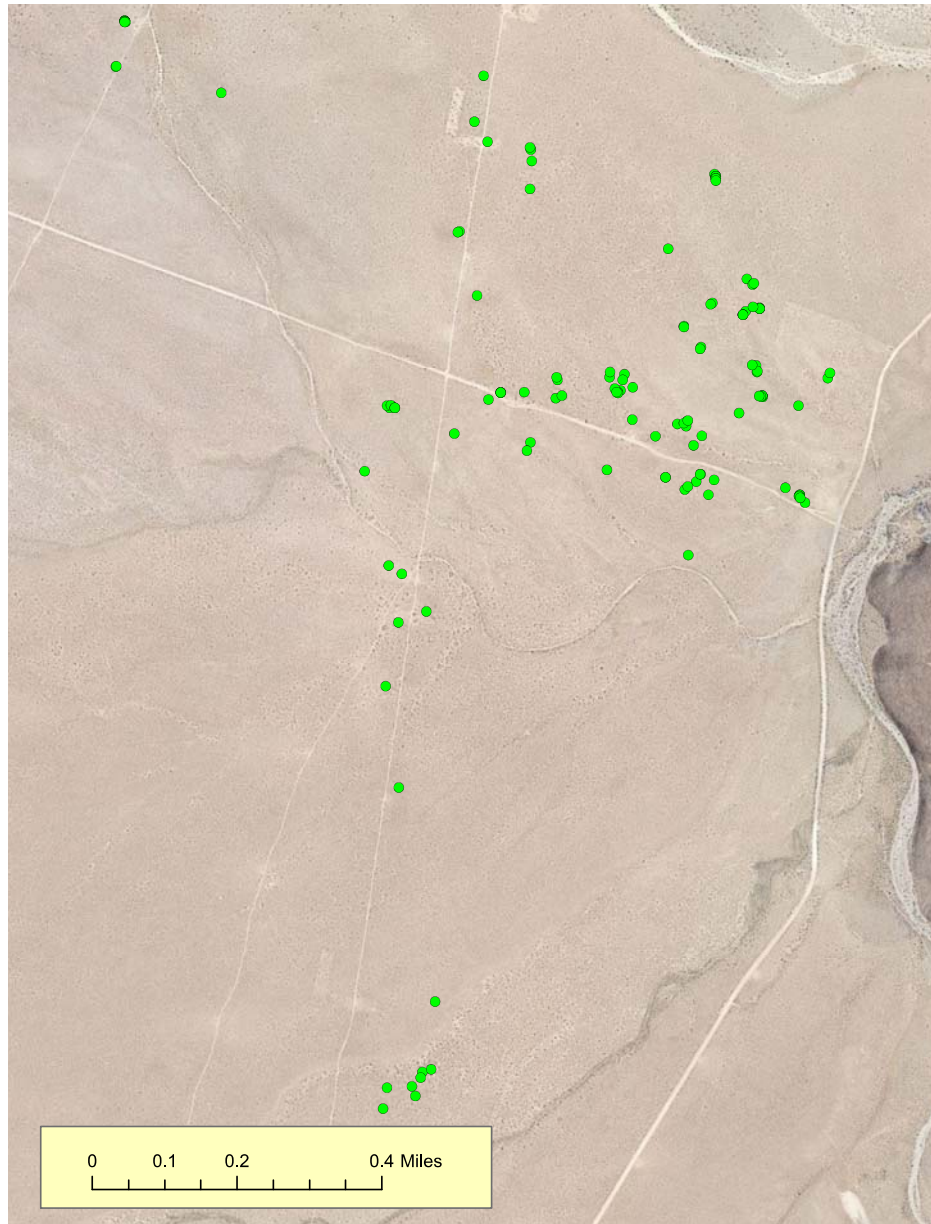
4.3.3 Simulation of changes in genetic diversity under climate change

A simulation approach was used to begin exploring the potential impact of climate change on population persistence, movement, and maintenance of genetic diversity. This approach is a spatially-explicit, individual-based method to assess the influence of the landscape on the

spatial distribution of genetic variation using the software CDPOP (Landguth and Cushman 2010). Specifically, how individual mating and dispersal behavior of MGS will lead to changes in population genetic diversity and structure under various climate scenarios was explored. To accomplish this, four separate MGS populations in the Freeman Gulch area under various scenarios of habitat availability were initialized: 1) the current distribution of habitat as identified in Chapter 2 with moderate land use, 2) a 'no land use' alternative to assess the impact of recent land use changes, 3) habitat availability under the A2 emissions scenario derived from 2030 climate under moderate land use, and 4) habitat availability under the A2 scenario derived from 2080 climate under moderate land. This was explored on a portion of the range that extends from Freeman Gulch into the northern portions of the range covering 13,758 km². The region captures a wide range of habitat suitability, is anticipated to experience dramatic changes in habitat suitability with climate change, and encompasses what is expected to be an important corridor connecting central and northern portions of the range (Chapters 2, 3, and 5). Due to analytical limitations of currently available software, the modeling effort could only include 1 adult individual per 1 km grid cell, while field data from Freeman Gulch suggest such highly suitable habitat may maintain ca. 7 individuals/grid cell. UNICOR software (Landguth and Cushman 2010) was used to calculate the cost-weighted distance between all cells. Maps of resistance were generated by inverting the habitat models produced in Chapter 2 (i.e., least suitable habitat has highest resistance to movement). Compensation for the lower-than-realistic densities was attempted by allowing individuals to search for mates and to disperse to a wider neighborhood than average movement distances that likely typify MGS. Nonetheless, the dispersal averages in the simulations (in Euclidean distances, see Results) were within what has been measured in the field (Harris and Leitner 2005), are largely consistent with the genetic autocorrelation estimates, and reflect the sex bias that appears in the genetic and field-based information. Mating and natal dispersal movements followed an inverse-square probability function, therefore movement thresholds were set in cost-distance units as follows: mating movement to 425 units, female dispersal to 220 units, and male dispersal to 850 units. Reproduction was sexual, allowed for multiple paternity, and fecundity followed a Poisson distribution with a mean of 5 offspring. Generations were non-overlapping. There were 17 loci that began with 16 alleles per locus (reflective of the most diverse locus in the empirical dataset) and genotypes were randomly assigned to individuals to begin the analysis with maximum genetic diversity. The mutation rate was set to 0.0005. There were 25 replicates of 500 generations under each scenario (Landguth *et al*. 2010, Wasserman *et al*. 2012). Based on reproduction and dispersal within the simulated population in the context of the 4 scenarios of habitat availability and landscape resistance, CDPOP recorded population size at each generation, total number of alleles, observed and expected heterozygosity, and resulting mating and natal dispersal distances in Euclidean distance.

To quantify the spatial distribution of genetic variation under each scenario, sGD (Shirk and Cushman 2011) was used to estimate Nei's genetic diversity index (Nei 1987). Estimated genetic diversity across genetic neighborhoods was encompassed by 425 cost distance units.

4.4 Results

4.4.1 Underlying correlates of genetic distance within *X. mohavensis*

Pairwise linearized F_{ST} ranged from a low of 0.008 between the nearby Freeman Gulch and El Paso Mountain localities (differentiation not significantly different from 0) to a high of 0.163 between Cactus Peak and Johannesburg (Table 7). As in previous similar analyses (Bell and Matocq 2011), Euclidean distance alone showed a significant relationship with genetic distance, but only accounted for a relatively small portion of the total variation (~ 15 percent in this analysis; Figure 24, Table 6). The use of cost-weighted distance and cumulative resistance increased the predictive power of the models from 15 percent to 17 percent and 25 percent, respectively (Figure 24, Table 6). Using barrier distance alone generated the strongest relationship with genetic distance and explained 27 percent of the total variation (Table 6). Using partial Mantel's tests to account for the effect of the course of the Owens River system as a barrier, none of the measures of habitat-based distance remained statistically significant (Table 6). The increase in predictive power gained by using cumulative resistance over cost-weighted distance is significantly greater (at α = 0.05) than the increase in predictive power gained by using cost-weighted distance over Euclidean distance, especially when the barrier effect is taken into consideration (Table 6).

Figure 24: Correlations between genetic distance and various measures of geographic and habitat-based distance.
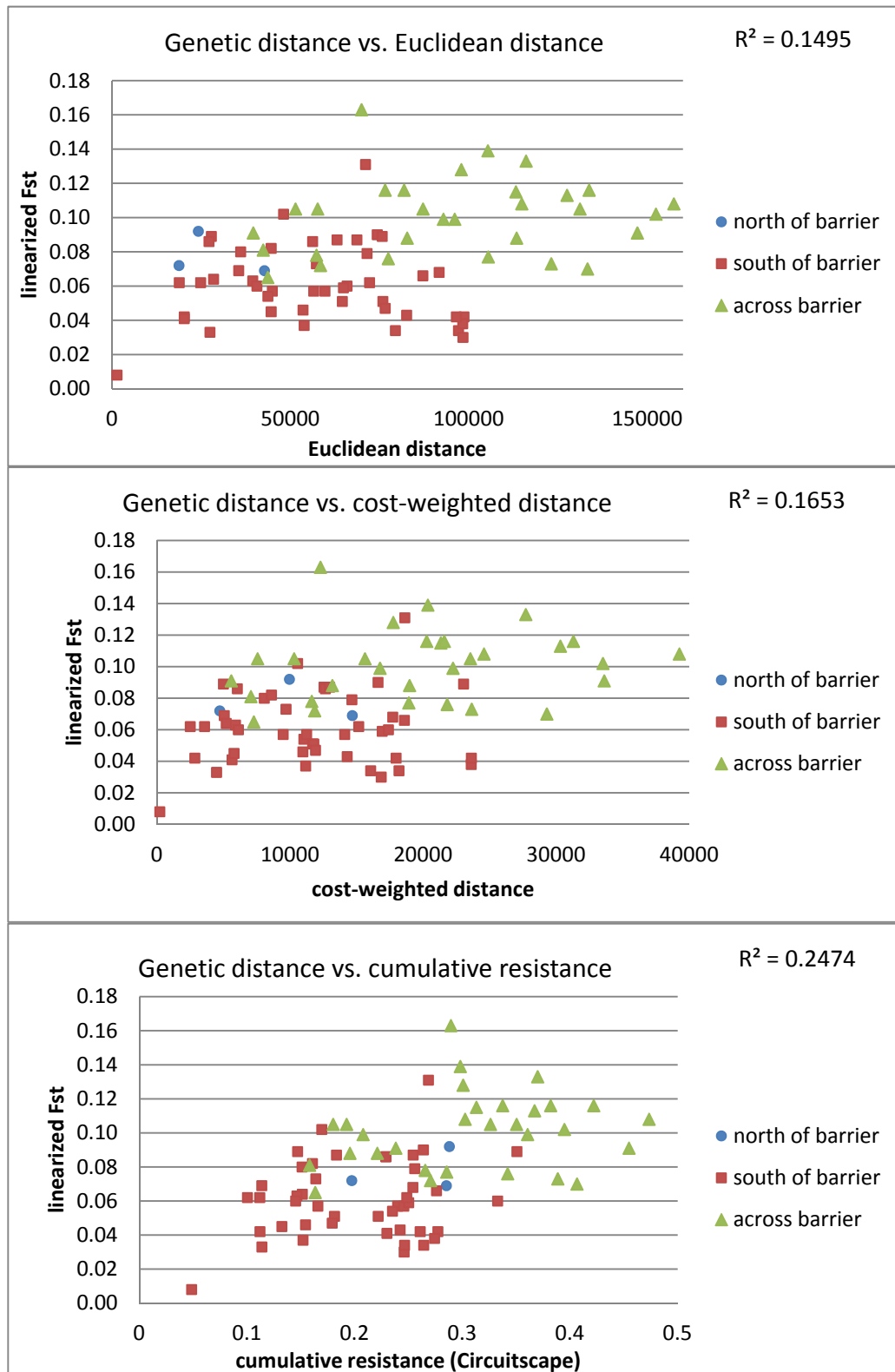
Table 7. Pairwise linearized FST between populations of *X. mohavenisis*.

	Olancha	Coso	Cactus	Frmn Gulch	El Paso	Johann.	Psn Cyn	DTNA	EAFB	Borax	Frmnt Pk	Coolg.	Ft Irwin
Olancha	0.000												
Coso	0.069	0.000											
Cactus	0.092	0.072	0.000										
Frmn Gulch	0.076	0.065	0.072	0.000									
El Paso	0.116	0.081	0.078	0.008	0.000								
Johann.	0.099	0.105	0.163	0.064	0.089	0.000							
Psn Cyn	0.116	0.091	0.105	0.057	0.054	0.086	0.000						
DTNA	0.133	0.088	0.128	0.063	0.060	0.082	0.079	0.000					
EAFB	0.102	0.088	0.105	0.051	0.047	0.087	0.066	0.045	0.000				
Borax	0.116	0.099	0.115	0.057	0.073	0.102	0.090	0.062	0.042	0.000			
Frmnt Pk	0.113	0.105	0.139	0.046	0.037	0.080	0.057	0.069	0.033	0.062	0.000		
Coolg.	0.108	0.108	0.070	0.042	0.038	0.131	0.089	0.068	0.059	0.062	0.086	0.000	
Ft Irwin	0.091	0.077	0.073	0.034	0.042	0.087	0.060	0.030	0.034	0.043	0.051	0.041	0.000

All pairwise values are significantly different from zero ($P < 0.001$) with the exception of Freeman Gulch and El Paso Mtns. Definitions for abbreviations include: Frmn – Freeman; Johann - Johannesburg; Psn – Poison; DTNA – Desert Tortoise Natural Area; EAFB – Edwards Air Force Base; Frmnt – Fremont; Coolg. – Coolgardie.

4.4.2 Fine-scale genetic structure: insight from Freeman Gulch

When including all Freeman Gulch individuals (N = 143) at 50 m distance classes, positive and significant spatial genetic autocorrelation is evident up to 150 m, with an x-intercept at 300 m (Figure 25A). Bins of 100 m and 25 m show positive and significant r-values up to 250 m and 150 m, respectively, with x-intercepts of 350 m and 170 m (Figure 25B, C). Intervals of 25 m across multiple distance classes were used to find positive and significant r-values through a distance of 1050 m (Figure 26A, Table 8). The juvenile class has a high level of genetic similarity at the smallest spatial classes and values remain positive and significant to a distance of 1100 m (Figure 26B, Table 8). In contrast, the adult class has limited power at the smallest spatial scales. Due to a lack of available comparisons at those scales, values are low, becoming significant and positive in the range of 225-425 m but then quickly declining (Figure 26B, Table 8). Combining juveniles and adults into female and male classes, there was a positive and significant correlation in both groups at the smallest spatial classes, but positive correlation in the males ceased at 350 m while it continues to 725 m in females. At the smallest distance bin of 25 m, average r is not different between females and males (0.23 versus 0.20), but at subsequent distance classes, genetic similarity among females is consistently greater than in males.

Figure 25. Autocorrelograms of the spatial scale of localized genetic structure in Freeman Gulch.
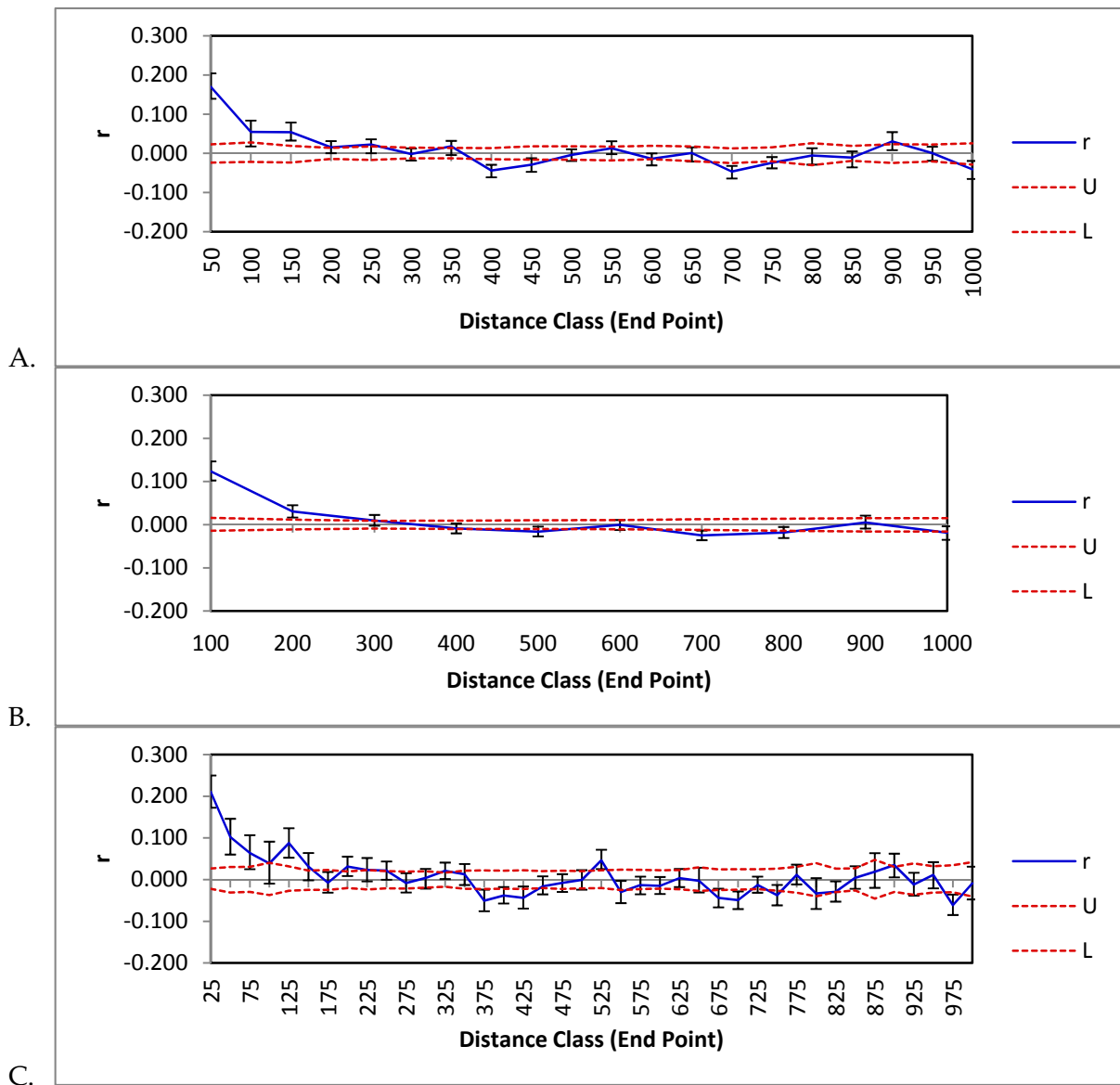
The x-axis shows various distance classes into which individual genotypes were grouped (A. 50m, B. 100m, C. 25m) and the y-axis shows the autocorrelation statistic r. Error bars that bound r show the 95% confidence interval determined by bootstrap resampling. Red dashed lines show the 95% confidence interval around the null hypothesis of no spatial structure determined by permutation.

Figure 26. Correlations across distance classes and categories. CI values as in Figure 25.

A. All
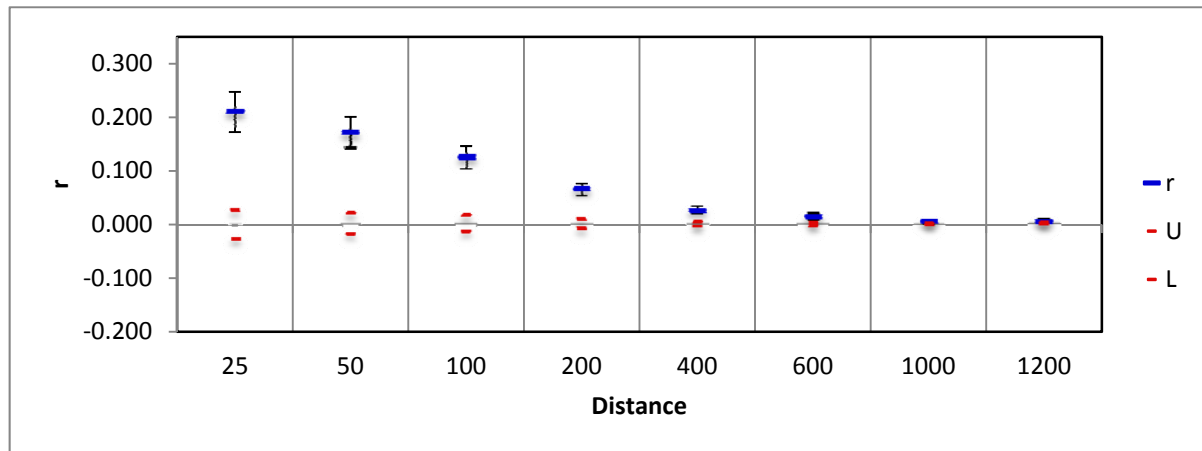
B. Juvenile and adult classes
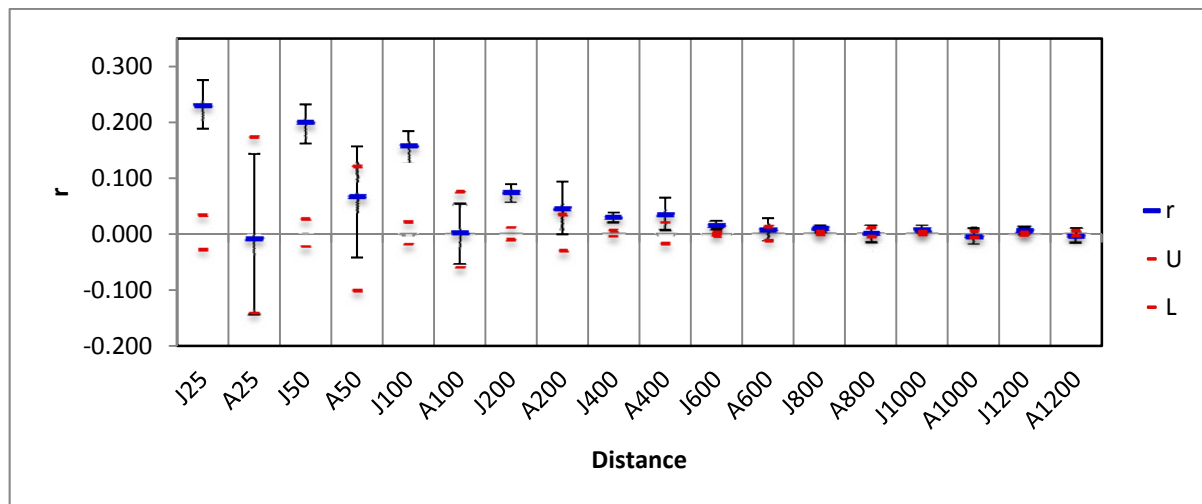
C. Female and male classes
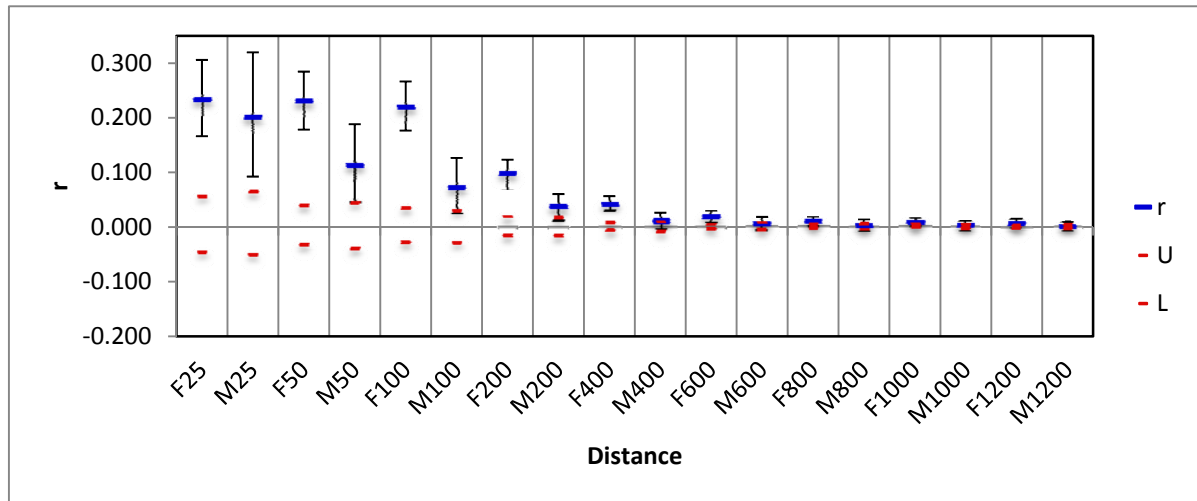
Table 8. Spatial autocorrelation in class sizes 25-1200 m.

Distance class	25 m	50 m	100 m	200 m	400 m	600 m	1000 m	1200 m
All								
n	150	244	407	1114	2881	4358	6162	6537
r	0.211	0.170	0.124	0.064	0.026	0.014	0.005	0.004
U	0.026	0.020	0.016	0.009	0.004	0.003	0.002	0.001
L	-0.026	-0.019	-0.014	-0.008	-0.004	-0.002	-0.001	-0.001
P	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Ur	0.247	0.201	0.146	0.076	0.033	0.019	0.009	0.009
Lr	0.172	0.141	0.102	0.053	0.019	0.008	0.001	0.000
Juveniles								
n	122	181	265	685	1701	2443	3114	3194
r	0.230	0.198	0.157	0.072	0.028	0.016	0.007	0.006
U	0.032	0.026	0.022	0.011	0.006	0.003	0.002	0.002
L	-0.028	-0.023	-0.019	-0.011	-0.005	-0.003	-0.002	-0.002
P	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Ur	0.276	0.232	0.184	0.089	0.038	0.024	0.014	0.013
Lr	0.189	0.162	0.130	0.055	0.019	0.008	0.001	0.000
Adults								
n	3	6	17	54	152	241	421	462
r	-0.010	0.065	0.002	0.045	0.034	0.007	-0.005	-0.004
U	0.173	0.120	0.073	0.035	0.020	0.012	0.006	0.005
L	-0.142	-0.102	-0.060	-0.032	-0.017	-0.012	-0.006	-0.005
P	0.540	0.117	0.475	0.007	0.001	0.105	0.944	0.956
Ur	0.144	0.157	0.052	0.094	0.065	0.029	0.011	0.011
Lr	-0.145	-0.042	-0.054	< -0.001	0.006	-0.014	-0.018	-0.017
Females								
n	46	81	119	341	921	1441	1943	2021
r	0.234	0.231	0.220	0.098	0.042	0.019	0.008	0.006
U	0.055	0.039	0.033	0.019	0.008	0.005	0.003	0.003
L	-0.047	-0.034	-0.029	-0.015	-0.007	-0.004	-0.002	-0.002
P	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Ur	0.306	0.285	0.267	0.123	0.057	0.029	0.016	0.015
Lr	0.166	0.178	0.177	0.070	0.030	0.008	-0.001	-0.002
Males								
n	24	43	73	209	456	616	940	1022

Distance class	25 m	50 m	100 m	200 m	400 m	600 m	1000 m	1200 m
r	0.202	0.113	0.073	0.036	0.010	0.005	0.002	0.000
U	0.063	0.044	0.030	0.017	0.009	0.007	0.004	0.004
L	-0.052	-0.041	-0.029	-0.016	-0.009	-0.006	-0.003	-0.003
P	0.001	0.001	0.001	0.001	0.009	0.071	0.152	0.377
Ur	0.320	0.188	0.127	0.060	0.026	0.018	0.011	0.010
Lr	0.092	0.044	0.024	0.012	-0.004	-0.008	-0.008	-0.009

Shown are pairwise comparisons *n*, correlation *r*, upper *U* and lower *L* bounds of the 95% CI around *r* = 0 (no spatial structure), probability *P* of positive autocorrelation (one-tailed test), upper *Ur* and lower *Lr* bounds around *r* estimated by bootstrap resampling.

4.4.3 Simulation of changes in genetic diversity under climate change

Each of the four-modeled scenarios led to dramatically different patterns of occupancy after 500 generations (Figure 27). The "present climate with no-land use" and "present climate with moderate land use" scenarios began with the largest distribution of animals and, after 500 generations, show occupancy of the majority of starting cells. After 500 generations, the no land use and modern scenarios have a potential number of suitable cells in the range of 2000 and 80 percent of these are occupied (Figure 28). In contrast, the A2 2030 and A2 2080 scenarios begin with reduced distributions of suitable habitat in comparison to the modern landscape and after 500 generations occupy little of their starting distributions (Figure 27). After 500 generations, the A2 2030 and A2 2080 scenarios are predicted to have only 45 percent and 24 percent of potentially suitable cells occupied, respectively (Figure 28).

Figure 27: Estimated squirrel occupancy based on CDPOP simulation results.
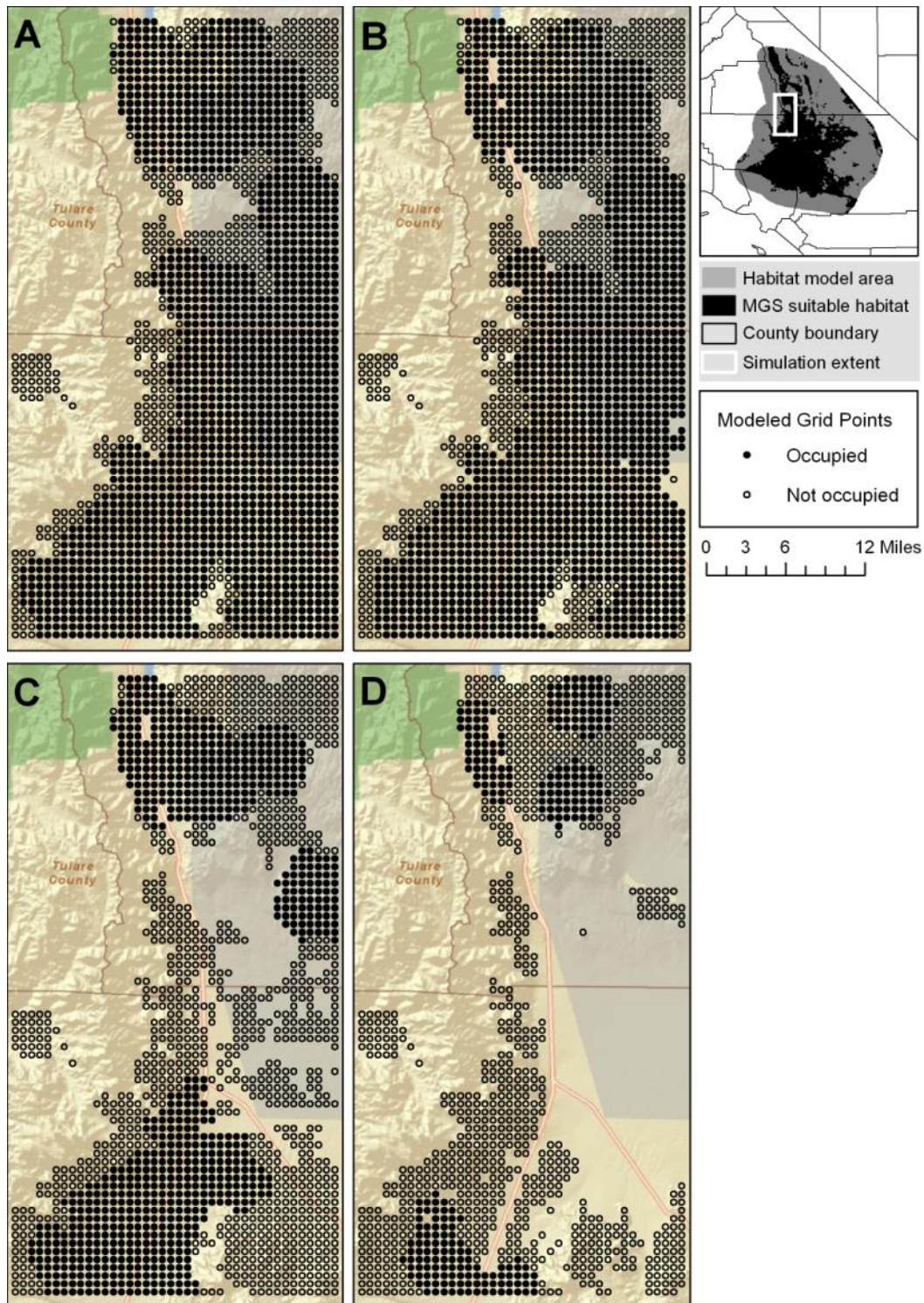
A) Occupancy derived from the no land-use estimation B) Occupancy derived using present-day climate with moderate land use C) Occupancy derived from the 2030 climate under the A2 emissions scenario with moderate land use D) Occupancy derived from the 2080 climate under the A2 emissions scenario with moderate land use

Figure 28: Number of suitable and number of occupied sites for each scenario as predicted by CDPOP simulations.
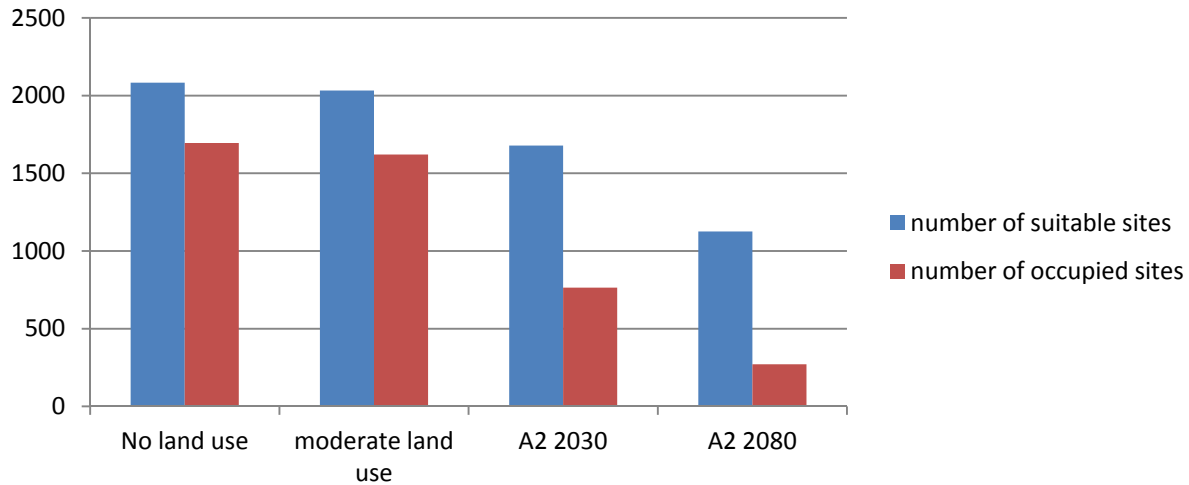
Scenarios include: present-day climate with no land use, present-day climate with moderate land use, 2030 A2 emissions with moderate land use, and 2080 A2 emissions with moderate land use.

Modeled results of mate-searching movements as well as female and male juvenile dispersal show progressive decline across the various scenarios of habitat availability (Figure 29). This decline is largely due to the increased landscape resistance to movement under each scenario. The A2 2030 and A2 2080 scenarios predict similar, relatively low values of individual movement. In contrast, much greater movement is possible under the modern scenario, with the least resistance to movement under the hypothetical no land use scenario. Even under the highest movement scenario (present climate with no land use), both male and female average dispersal distances are at the high end of what likely characterizes MGS, but within values directly observed in the field (Harris and Leitner 2005).

Figure 29: Estimated individual movement, under 4 habitat suitability and landscape resistance scenarios: present-day climate with no land use (present/NLU), present-day climate with moderate land use (present/MLU), 2030 A2 emissions with moderate land use (A230/MLU), and 2080 A2 emissions with moderate land use (A280/MLU).
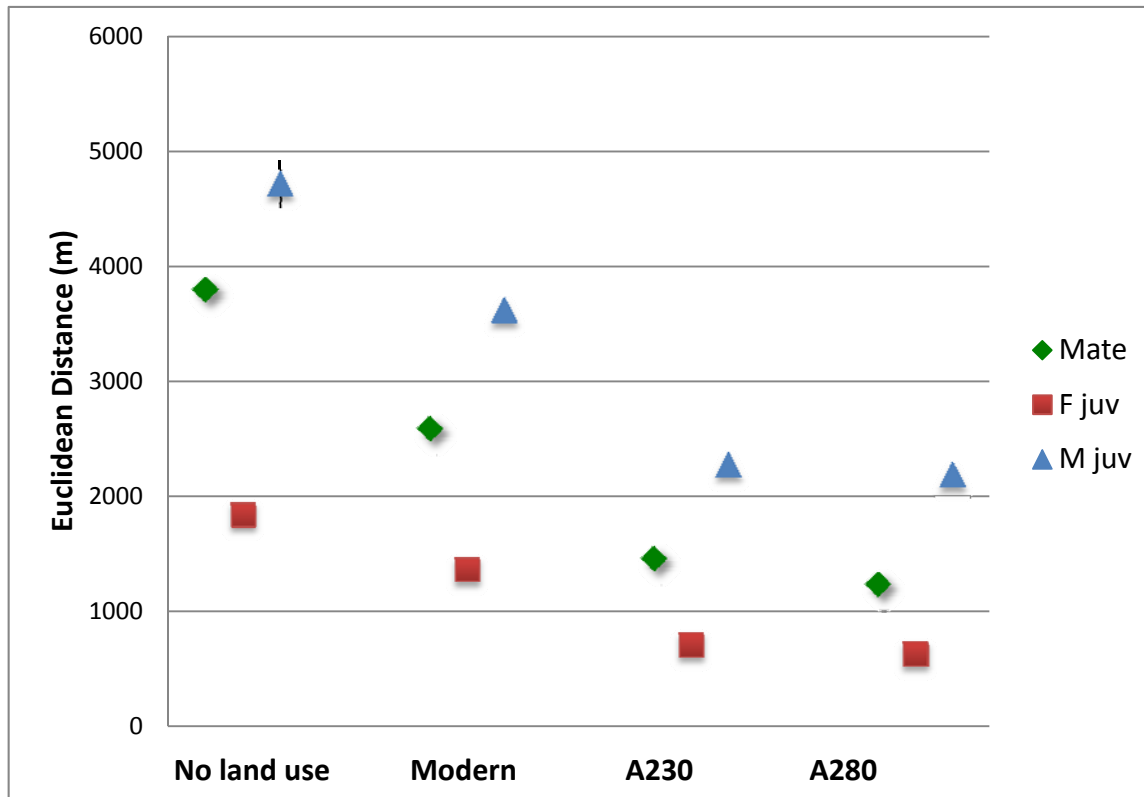
Means and standard deviations are taken from 25 replicates of 500 generations. Standard deviations that are not visible are smaller than the symbol showing mean values.

In concert with the patterns of occupancy (Figure 27), population size is greatly reduced under either future-climate scenario in comparison to either present climate scenario (Figure 30). Likewise, the total number of alleles across all 17 loci is greatly reduced under future scenarios. Each scenario began with maximal diversity of 16 alleles at 17 loci for a total of 272 alleles, meaning that the present climate scenarios retained approximately 65 percent of starting diversity, while the A2 2030 and A2 2080 scenarios retained 42 percent and 26 percent, respectively. In terms of average observed heterozygosity, the present climate scenarios predict 51-56 percent heterozygosity while the A2 2030 predicts 21 percent and the A2 2080, 4 percent.

Figure 30: Estimated population size, number of alleles, and heterozygosity under 4 habitat suitability and landscape resistance scenarios: present-day climate with no land use (present/NLU), present-day climate with moderate land use (present/MLU), 2030 A2 emissions with moderate land use (A230/MLU), and 2080 A2 emissions with moderate land use (A280/MLU).
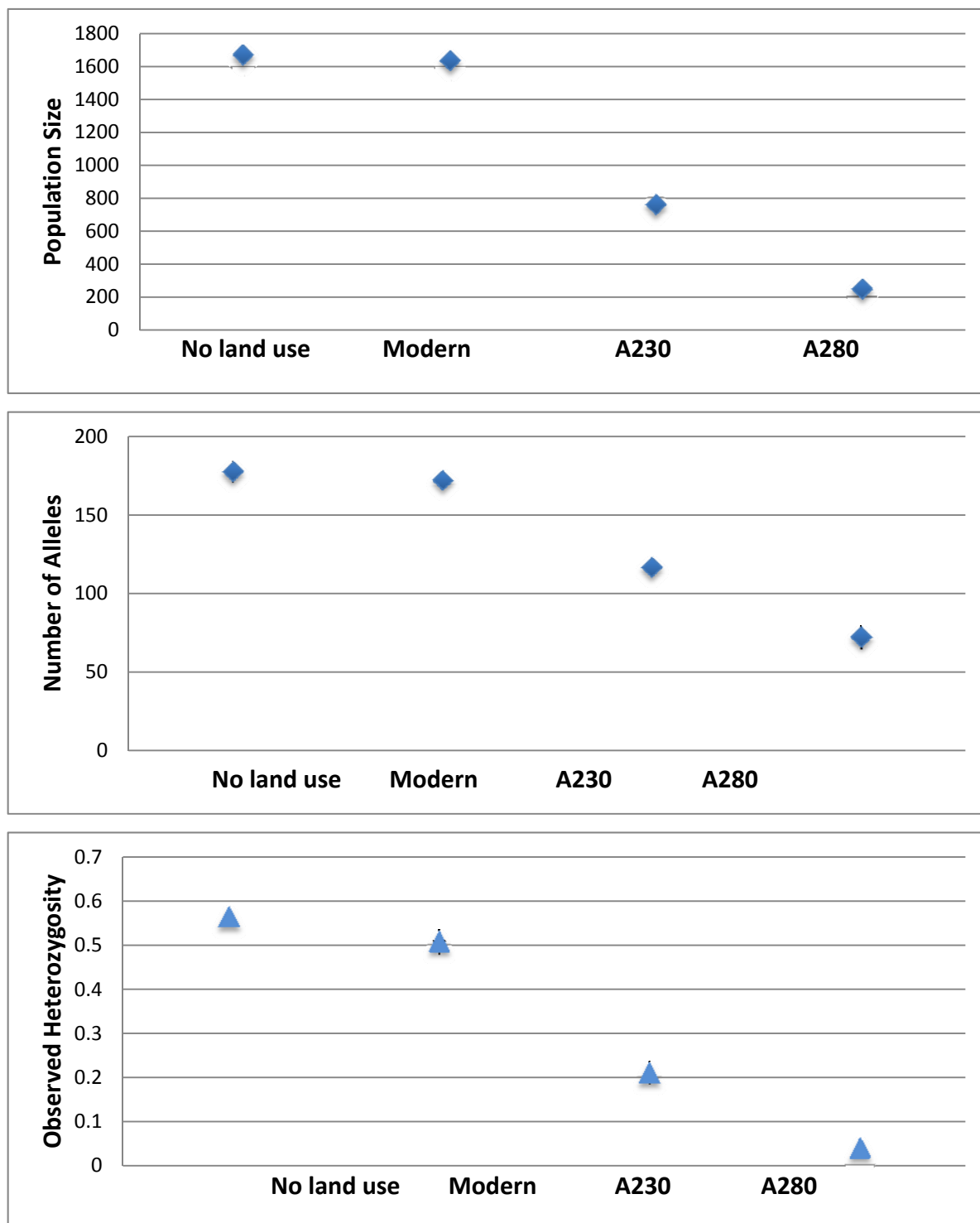
Means and standard deviations are taken from 25 replicates of 500 generations. Standard deviations that are not visible are smaller than the symbol showing mean values.

The spatial distribution of genetic diversity within each scenario shows marked differences in regional diversity (Figure 31). The most continuously occupied distribution under the "present climate with no land use" scenario shows the large block encompassing the Freeman Gulch region maintaining relatively high levels of diversity while the smaller, relatively isolated northern block is predicted to have lower levels of diversity, despite relatively high predicted occupancy (Figure 31A). The modern scenario (Figure 31B) shows a relatively more fragmented landscape but the highest levels of diversity are again predicted in the Freeman Gulch area with progressively lower diversity to the north. The A2 2030 scenario predicts low genetic diversity in the few remaining fragments, while the A2 2080 scenario has such sparse distribution of individuals that few localities even allowed estimation of local genetic diversity due to small sample sizes.

Figure 31: Nei's gene diversity index for occupied occurrence points with 5 genetic neighbors or more.
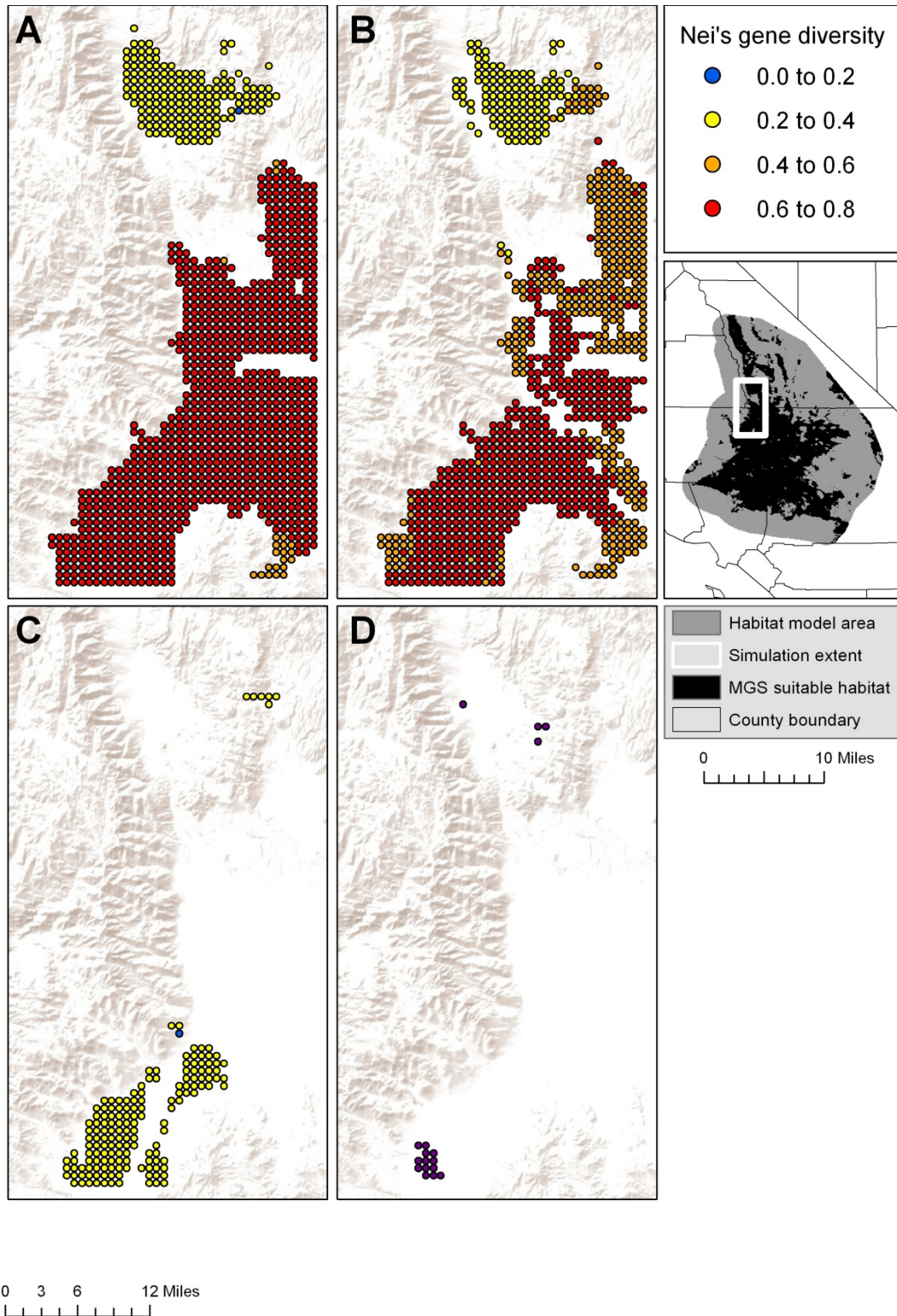
A) present-day climate with no land use B) present-day climate with moderate land use C) 2030 A2 emissions scenario with moderate land use D) 2080 A2 emissions scenario with moderate land use.

4.5　Discussion

The current genetic variation that characterizes a species is the result of both historic and ongoing processes. Understanding the interplay between historic and ongoing factors in determining the generation and maintenance of genetic variation requires study at multiple spatial scales using various parts of the genome that evolve at different rates, providing insight into different temporal depths of history. With the newly available information reported in earlier chapters of this report, there is an unprecedented opportunity to view genetic variation in *X. mohavensis* within the context of habitat suitability and connectivity to extend the current understanding of factors influencing the maintenance of diversity in this system, as well as to clarify research priorities that will allow the greatest use of the new information.

4.5.1　Barriers and habitat as predictors of genetic distance among populations

Pairwise genetic distance among populations of *X. mohavensis* are not well explained by the straight-line geographic distance among sampling localities (Bell and Matocq 2011; Figure 24). The first habitat-based estimate of distance between localities reflected the path containing the most suitable habitat. However, this least-cost path resulted in a non-significant improvement in the relationship with genetic distance in comparison to simple straight-line distance. This is due in large part to the high correlation between straight-line distance and cost-weighted distance ($r^2 = 0.742$) because large portions of the distribution, especially in the south, are identified as suitable habitat. As such, the least cost path can often resemble the shortest straight-line route between two localities. Overall, the low levels of population differentiation that characterize *X. mohavensis*, especially across the southern end of the distribution, suggest that gene flow has likely been quite high across large portions of the range, which is consistent with what appears to be contiguous areas of largely suitable habitat (Chapter 2). On the other hand, cumulative resistance across the landscape, as estimated by circuit theory (McRae 2006), does lead to significant improvement in explaining variation in genetic distance among localities. This suggests that localities that are connected by multiple potential routes experience more genetic exchange over time. Indeed, circuit theoretic models may be most appropriate at the multi-generational scales of the current population samples because they incorporate the existence of multiple pathways and dimensionality that is likely important at this scale (Spear *et al*. 2010). Again, taking the southern portion of the distribution as an example, localities across this region can often be connected by multiple routes through currently suitable habitat, which appears, over time, to have augmented genetic connectivity.

While gene flow among populations appears to be partly facilitated by the distribution of the current measure of suitable habitat, a very strong correlate of current differentiation among populations is that associated with the course of the Owens River system. This factor alone explains more of the variation in genetic distance between populations than any other distance measure evaluated (even when the influence of other distance measures is partialled out), and when its influence is removed, none of the other distance measures remain statistically significant.

The history of the Owens River system is quite well understood. Throughout the Pleistocene snowmelt filled Owens Lake, which overflowed into the river system and flowed south to fill China Lake, which then overflowed to fill Searles Lake, and so on to flood Panamint Lake in particularly high flow years (Smith 2009). This repeated flooding occurred throughout Pleistocene times but may have even occurred beyond the start of the Holocene (*c.* 12,000 years ago) with a final apparent pulse *c.* 2-3,000 years ago (Smith 2009). Diversification within *X. mohavensis* appears to have been strongly influenced by these dynamics with the deepest genetic subdivisions within the species, as measured by both mitochondrial and nuclear deoxyribonucleic acid (DNA), mapping to this region and temporal genetic estimates suggest expansion or re-expansion into the range north of this river course occurring *c.* 11.7 thousand years ago. While the microsatellite data suggest there has been more recent admixture between the northern genetic group and more southern populations, the relatively minimal amount of apparent genetic exchange suggests that while an actual riverine/lake barrier no longer exists in the area, it may still present a filter, if not an actual barrier, minimizing gene flow across this area in recent and perhaps current times. Unfortunately, the ability to characterize gene flow across this area remains limited because of the minimal surveying and sampling that has been done in the area, most notably across China Lake. This area encompasses an important gap in the knowledge of the current distribution of the species and warrants further survey efforts.

It is important to note again that the spatial distances between the current sampling localities of *X. mohavensis* greatly exceed individual dispersal capacities, and even if connected by recent gene flow, would be averaged across multiple generations of dispersal and across a great deal of habitat heterogeneity. It is quite possible that the relationship of genetic distance with habitat suitability and landscape connectivity (Chapters 2 and 3) would be stronger with refined spatial sampling of genetic variation (Murphy *et al*. 2008). Alternatively, gene flow may be related to particular habitat or landscape variables at the current resolution of analysis, but those variables may not be included in the current habitat model. Finally, it is also possible that gene flow is not particularly facilitated or hindered by habitat variables and that it occurs at a consistent scale and rate, even though habitat that would otherwise be considered unsuitable (Harris and Leitner 2005).

In order to appropriately infer any causal relationship between gene flow and landscape variables, it is imperative to couple the spatial resolution at which gene flow occurs with the resolution of potentially important landscape and habitat variables (Cushman and Landguth 2010b, Anderson *et al*. 2010). Ideally, the grain at which landscape data are collected would be smaller than the dispersal distance of the focal taxon (Fortin and Dale 2005, Anderson *et al*. 2010). As such, to guide future sampling efforts of both genetic variation and habitat features, it is important to identify the spatial scale of localized movement and gene flow in *X. mohavensis*. Such an analysis was conducted on samples collected in the Freeman Gulch area allowing an examination of genetic patterns at the finest spatial scale, that is, beginning with nearest neighbors, then encompassing an extent that would presumably capture a large portion of individual dispersal and, finally, extending beyond probable individual dispersal.

4.5.2 Fine-scale population genetic structure in *X. mohavensis*

Patterns of genetic spatial autocorrelation can provide insight into the scale of localized movement and gene flow and can identify how different segments of a population contribute to the distribution of genetic variation (Peakall *et al*. 2003; Double *et al*. 2005; Banks and Peakall 2012). The analysis of *X. mohavensis* shows significant positive local genetic structure. Examining these patterns at multiple scales, detectable positive genetic structure was found to extend to >1 km in the Freeman Gulch area. There was not enough power to examine patterns of genetic structure in the adult population only, but in combining the age classes, there do seem to be distinct patterns between the sexes. Females show a spatial extent of positive genetic structure to 725 m while positive structure in males extends to only 350 m. This is consistent with the observation that males, on average, disperse further than females (Peakall *et al*. 2003). Consistent with this interpretation is the fact that *r*-values in females are higher than in males in all significant distance bins, with the exception of the smallest bin. The interpretation of high genetic similarity in both males and females at the smallest bin class is that this distance category captured very young juveniles, still in the presence of litter-mates, and perhaps, their same-sex parent (Double *et al*. 2005; Beck *et al*. 2008).

A pattern of overall positive spatial genetic autocorrelation, declining to zero and then oscillating from negative to positive (as seen in Figure 24) is consistent with an hypothesis of restricted gene flow (Epperson *et al*. 1999, Banks and Peakall 2012), however, other factors could contribute to positive fine-scale genetic structure (Peakall *et al*. 2003). Social structure that would result in the spatial clustering and limited dispersal of related individuals could be contributing to the observed patterns, although known spatial clustering of relatives in Richardson's ground squirrels actually led to fine-scale negative structure (van Staaden *et al*. 1996), rather than the positive patterns observed here. The results are also heavily influenced by the pulse of young-of-the-year, which can contribute to positive local structure. Given that young animals were tagged throughout the above-ground season, some would have been tagged at their natal site, while others would have been first encountered post-dispersal. Animals caught in the pre-dispersal stage may contribute to positive structure in the smallest distance bin because patterns between males and females here are indistinguishable. However, the post-dispersal animals, through their relatedness to each other and resident adults, contribute to positive structure beyond the smallest bins. As such, these young animals may provide a good estimate of the spatial scale of localized natal dispersal. While these young dispersers contribute heavily to the patterns discovered here, positive spatial genetic autocorrelation is expected to be the result of multi-generational gene flow, and not only relationships among natal dispersers. As such, if this pattern is maintained temporally, it would suggest that average effective dispersal may occur at an extent of >1 km.

While the relationship between dispersal and gene flow is expected to be quite strong (Bohonak 1999), there are a number of factors that could cause a discrepancy between direct (*i.e.,* telemetry or mark-recapture) and indirect (*i.e.,* genetic) measures of movement. Importantly, the genetic estimate of the spatial extent of local population structure (>1 km) is consistent with direct estimates based on radio-collared individuals and an extensive mark-recapture effort (Harris and Leitner 2005). Harris and Leitner (2005) found that male dispersal distances (mean =

2.9 km, range = 390 m – 6.2 km) exceeded that of females (mean = 753, range = 0 – 3.9 km) and that average dispersal distances were approximately 1.7 km (range 0 – 6.2 km). Further analyses are required to clarify the spatial scale of gene flow in MGS in a range of habitat types and under various demographic conditions. Nonetheless, the broad spatial extent of positive genetic structure, as evidenced by both genetic and direct estimates, has important implications concerning the potential impact of habitat fragmentation on the population and dispersal dynamics that naturally maintain fine-scale genetic diversity in MGS.

Although the spatial-autocorrelation approach demonstrated here has the potential to provide critical insight into fundamental ecological and evolutionary processes occurring within MGS, future fine-scale genetic sampling efforts will be strengthened by 1) coupling them with fine-scale habitat measurements that could then be correlated with genetic similarities among individuals to gain insight into features that may facilitate or restrict gene flow, and 2) including additional localities to represent a breadth of habitat and population types (e.g., hypothesized suitable versus less suitable habitat; potential source versus sink populations). As the authors' first view of fine-scale genetic structure in MGS, it is important to note that Freeman Gulch is a location that has been consistently occupied by these animals, leading to the recognition of this site as a 'core population' (Leitner 2008). In the habitat suitability model (Chapter 2) the Freeman Gulch area appears to contain highly suitable habitat, which is consistent with its history of population persistence. Future analyses in a range of habitats and under various population dynamics will be important to place the Freeman Gulch patterns into what might be a broad spectrum of dispersal and gene flow capabilities. Ultimately, long term assessment of temporal variation in local genetic structure along with detailed demographic studies will be needed to allow further resolution of the interplay between dispersal, mating system, population dynamics, and habitat variables in determining fine-scale genetic structure in this species.

4.5.3   Simulated response to climate change

The process modeling approach required synthesis of information across all project components including habitat models (Chapters 2 and 3), landscape connectivity (Chapter 5) and genetic structure (current chapter). Each of the four modeled scenarios of habitat availability and suitability in the Freeman Gulch area led to dramatically different distributional patterns under the dispersal and mating parameters explored here. While the present climate scenarios showed continued occupation of the majority of currently occupied areas after 500 generations, the A2 2030 and A2 2080 scenarios show dramatic loss of site occupancy across the modeled range. Likewise, tracts of broadly occupied lands, such as those characterized by the modeled portions of the Freeman Gulch area, maintain relatively high levels of genetic diversity, while the A2 2030 and A2 2080 scenarios show dramatic losses of variation and local fixation throughout the range. It would appear that the limited availability of suitable habitat coupled with relatively high resistance of the landscape (due to lowered suitability), could decrease movement and local persistence to a level that there is overall collapse of the population under either future climate scenario. Thus, the predicted effects of climate change on future MGS patch occupancy are yet more negative than the predicted effects on the availability of suitable habitat, given that

the process model simulations predict very limited ability to disperse to isolated habitat patches.

These initial explorations of MGS response to potential climate change should be interpreted with great caution. First, all the caveats given in previous chapters of this report apply to the outcomes of this analysis including: limitations of the ability to estimate habitat suitability, uncertainty of what these values mean in terms of MGS population dynamics and movement across the landscape, and the degree of uncertainty in future climate scenarios. Furthermore, the ability to simulate individual response to landscape resistance and to estimate its genetic consequences is very new (Landguth and Cushman 2010), so analytical and computational limitations still minimize the ability to characterize MGS biology. Nonetheless, efforts to provide a framework upon which future analyses can be built will improve as current limitations are overcome. Specifically, for MGS, it will be critical for future simulations to reflect realistic densities (and their variation), mating and juvenile dispersal movements, and yearly variation in reproductive output. It will also be important to take into account other behavioral or physiological plasticity that might allow individuals and populations to persist in warming climates (Kearney *et al*. 2009). In the case of MGS, they appear to already exist close to their physiological limits in the current environment; however, their capacity to use microrefugia may confer resistance and resilience beyond current knowledge to model at this time.

The climate change models that were examined show suitable MGS habitat expanding in the northern-most reaches of the range, and although not modeled here, potentially expanding well north of the current range in the valleys immediately east of the Sierras. Nonetheless, the initial simulations suggest that in the anticipated short timespan to substantive climate change, MGS may not have time to naturally colonize and expand into these regions before being effectively extirpated from their current range. Both direct and indirect estimates of dispersal suggest that this species has unusually high capacity for movement, but making adequate predictions of whether these dispersal capabilities will be able to match the pace of climate change awaits refinement of the ability to model climate change and MGS response to changing conditions.

The process modeling approach could also be used to explore the potential impact of various energy development scenarios (Chapter 5). While relatively little is known of the impact of energy development on wildlife populations (Lovich and Ennen 2011), the habitat loss and fragmentation that could be associated with development would be expected to augment isolation among populations, potentially leading to increased genetic drift and inbreeding within isolates (Keyghobadi 2007). Variables such as facility footprint, quality of habitat on and surrounding a site, and presence of other barriers to movement associated with individual projects (e.g., fences) would have different impacts on population sizes and connectivity among populations, and thus, expectations of changes in genetic diversity and subdivision.

CHAPTER 5:
Landscape connectivity of the Mohave ground squirrel

By Thomas E. Dilts, Peter J. Weisberg, Marjorie D. Matocq, Philip Leitner, Kenneth E. Nussear, Todd C. Esque, and Richard D. Inman

5.1 Introduction

Estimates of potential habitat provide a useful starting point for defining critical areas for Mohave ground squirrel (MGS, *Xerospermophilus mohavensis*) conservation, but do not address the relative importance of habitat patches for facilitating MGS movement through the landscape. Landscape connectivity analysis is needed to quantify the importance of habitat for MGS dispersal and movement processes. Given global change predictions (climate change, urbanization and other development, invasive species, etc.), maintenance of landscape connectivity is critical for allowing species to respond to changing habitat configurations. In addition, animal movement processes are critical for maintaining genetic diversity and for fostering species persistence through metapopulation processes, where local extirpation can be balanced through recolonization. Given global change predictions, maintenance of landscape connectivity is critical for allowing species to respond to changing habitat configurations. In concert with a variety of other land uses, current and planned energy developments not only threaten to reduce habitat area, but may impede the ability of MGS to move to suitable habitat as climate changes through the 21st century and beyond.

In order to make informed conservation planning decisions towards the goal of maintaining viable MGS populations, a robust procedure for habitat prioritization is needed that considers the entire network of habitat. The size and position of a habitat patch within the greater habitat network may strongly influence its role in maintaining connectivity at the landscape level (Minor and Urban 2007). For example, a large habitat patch that provides adequate habitat to support a MGS population may be less subject to local extirpations and may serve as a source of emigrants to replenish other areas that have suffered extirpations (Table 9; see also Rudnick *et al*. 2012 for further description of these terms). If a large habitat patch is isolated, its connectivity role will be limited compared to a patch that is centrally located and well-connected (Estrada and Bodin 2008). Furthermore, some habitat areas that do not support large populations provide important connections among critical source populations. These "stepping-stone" areas often have a disproportionately large role in supporting overall habitat network connectivity and should be considered for conservation prioritization due to their value for facilitating movement that may exceed their habitat value (Saura and Rubio 2010).

Two previous efforts to prioritize critical connectivity areas in the Mojave Desert do not explicitly focus on MGS. The California Essential Habitat Connectivity Project (CEHCP, Spencer *et al*. 2010) assessed connectivity between blocks of wild land across the state of California. This

Table 9: Glossary of terms used in this chapter.

Term	Meaning	Source
Patch	Relatively homogenous area of habitat that differs from the surrounding matrix of non-habitat. The patch-matrix model contrasts with the gradient model in which habitat varies gradually and sharp distinctions between habitat and non-habitat do not occur.	McGarigal and Cushman 2005
Resistance surface	Alternatively known as a friction surface or cost raster. A resistance surface is a map that describes the impedance to movement as a species moves through the landscape. High resistance values indicate that movement is difficult while low values indicate higher potential for movement. Resistance surfaces provide the input for least-cost and circuit analyses.	Adriaensen *et al*. 2003
Least-cost analysis	Analytical approach that uses Dijkstra's algorithm to search for a single optimal "least-cost" path between two points that minimizes cumulative cost encountered along that path. "Cumulative cost" can be related to biological constraints such as energy expenditure or exposure to predation risk.	Adriaensen *et al*. 2003
Cost-weighted distance	The sum of all resistance values intercepted by the least-cost path.	Adriaensen *et al*. 2003
Cumulative resistance	In contrast to cost-weighted distance, which utilizes a single optimal path, cumulative resistance describes the distance between two points considering all potential paths simultaneously. The presence of multiple pathways increases the likelihood that "random walkers" will find their way between two points. Cumulative resistance is calculated using methods borrowed from electronics based on circuit theory.	McRae 2006
Cumulative current	Cumulative current can be used to predict the net movement probabilities through a particular raster cell. Habitat configurations with multiple movement pathways decrease current while a single movement pathway will increase current by effectively funneling random walkers.	McRae 2006
Graph theory	Mathematical method for the analysis of network problems. A habitat graph describes the spatial structure among and between habitat patches. Graph theory provides methods for assessing the importance of individual habitat patches in relation to all other habitat patches.	Urban and Keitt 2001
Node	Habitat patches are represented as one dimensional elements on the graph and may be weighted by habitat area or quality.	Urban and Keitt 2001
Link	Alternatively known as edges or connectors. Links represent the degree of connectivity between nodes through the matrix. Connectivity may be based upon cost-weighted distance, cumulative resistance, or simulated movement.	Urban and Keitt 2001
Probability of connection index (PC index)	An index that describes the importance of patches in upholding network connectivity. The PC index assess connectivity by iteratively removing patches and re-calculating the likelihood that two randomly placed animals can reach one another given the habitat configuration.	Saura and Pascual-Hortal 2007
PCconnector index	The probability of connection index can be parsed into three fractions – intra, flux, and connector. The connector fraction (PCconnector index) describes the importance of a patch for facilitating movement through the patch to access other patches.	Saura and Rubio 2010
Stepping stone	A habitat patch with a high PCconnector value that facilitates movement between other patches in the network. A stepping stone has a disproportionately large role in upholding network connectivity because of its geographic location.	Saura and Rubio 2010
Equivalent connected area EC_{PC} index	The size of a single maximally connected habitat patch that would provide the same probability of connectivity that the actual habitat network provides. Usually the equivalent connected area is less than the actual habitat area because connectivity among actual habitat is limited.	Saura *et al*. 2011
Minimum spanning tree	A graph consisting of the minimum number of links necessary to fully connect all nodes so that the graph consists of a single connected component.	Urban and Keitt 2001

study did not identify habitat for any species in particular, but instead used blocks of land that were deemed "natural." These natural landscape blocks were delineated and connected using resistance surfaces (Table 9), which were generic maps based on land cover rather than habitat needs. Resistance surfaces were derived from land cover and land protection status based upon expert opinion. Least-cost analysis (Table 9) was used to select an optimal route through the resistance surface and a corresponding corridor network was chosen that best connected the landscape blocks. This approach was coarse in its scale, and identified suitable areas that might provide connections between large natural blocks of land. However, it did not consider focal species nor were the resistance maps based on biological data such as animal movement or genetic data.

A second study – A Linkage Network for the California Desert (Penrod *et al*. 2012) – overcame many of the limitations of the first study by using focal species and expert-based habitat models that were constructed in a geographic information system (GIS). Focal species included bighorn sheep (*Ovis canadensis*), desert tortoise (*Gopherus agassizii*), kit fox (*Vulpes macrotis*), and badger (*Taxidea taxus*). Similar to the CEHCP, landscape blocks were defined based on protection status. Least-cost paths and their surrounding corridors were delineated based on expert-derived resistance surfaces combining land cover with topographic data such as elevation, slope, aspect, topographic position, as well as distance to streams and road density. However, none of the focal species identified by Penrod *et al*. (2012) appear to be suitable surrogates for MGS, and corridors delineated using the four focal species tends to connect mountain ranges rather than valley bottoms. Therefore, the linkage network proposed by Penrod *et al*. (2012) may be of little conservation value for MGS because of its differing habitat needs compared to the focal species that they used.

The two connectivity modeling efforts mentioned above were limited by the fact that expert opinion was used to construct the resistance map rather than biological data, such as the location of species occurrences, animal movement data, and/or genetic data; and they did not allow for changing patterns of habitat in response to climate change scenarios. Climate change has the potential to alter locations of important corridors that connect core populations and should be explicitly accounted for in reserve design strategies (Araújo *et al*. 2004, Vos *et al*. 2008).

Graph theory (Table 9), a powerful method for quantifying habitat connectivity, has been applied to numerous taxa and conservation applications (reviewed in Urban *et al*. 2009). Approaches derived from graph theory have the potential to simultaneously consider all parts of the habitat network regardless of land protection status. Graph theoretic approaches offer the most insight into habitat connectivity relative to the time and data costs required for other approaches, such as metapopulation modeling (Calabrese and Fagan 2004). One particular strength of graph theory is that it holistically considers the entire habitat network, thus it can be used to develop prioritization and ranking of habitat patches for conservation (Minor and Urban 2008). Species distribution models by themselves cannot be used for such a prioritization because they lack an explicit topological reference. Methods such as least-cost analysis (Adriaensen *et al*. 2003) and circuit theory (McRae 2006) are useful for determining the degree of connectivity between pairs of patches, but they are limited in prioritizing and ranking patches because they do not consider the entire habitat network. Another advantage of the graph

theoretic approach is that numerous indices exist for describing the relative position and importance of habitat nodes and connections within the overall network or within subsets of the graph (Urban and Keitt 2001). Different indices may relate to different roles that patches provide for supporting network connectivity (Bodin and Saura 2010).

A comprehensive spatial analysis of MGS landscape connectivity is developed across the entire range of the species, under current conditions and various future scenarios representing climate change and energy development. This analysis builds upon the habitat modeling component of the project (Chapters 2 and 3, this report) and derives a model of landscape connectivity from the habitat models. This analysis also informs the landscape genetics analysis (Chapter 4, this report) by developing maps of resistance to movement that are subsequently compared to genetic distance. The objectives are to:

(1) Identify critical areas for connectivity, considering dual roles of habitat patches as sources of dispersers and as stepping-stone patches or key corridors;

(2) Explore uncertainty in how hypothesized effects of land-use impacts, including urban areas, roads and agricultural lands, affect landscape connectivity;

(3) Model potential effects of climate change scenarios on future landscape connectivity;

(4) Identify important corridors for facilitating MGS distributional shifts in response to predicted climate change;

(5) Model potential effects of planned energy development on MGS landscape connectivity, given current climate conditions as well as future climate change scenarios.

5.2   Methods

5.2.1   Overview of the approach

A modified graph theoretic approach was used to assess connectivity in MGS habitat in the study area (Figure 32). Graph theory assesses connectivity by assuming that the landscape exists as a canvas of unsuitable habitat interspersed with patches of suitable habitat (Bunn *et al.* 2000, Urban and Keitt 2001, Minor and Urban 2008). Patches of habitat are referred to as nodes, and the connections between them are called links such that individuals disperse among nodes via links. It is assumed that the matrix surrounding habitat connections is unsuitable for the long-term persistence of a species and can only be used by individuals for dispersal (Wiens 1997), although the permeability of the matrix can vary greatly (Gustafson and Gardner 1996).

Unlike most previous studies using graph theory to assess habitat connectivity, a matrix of suitable and unsuitable habitat was not used. Instead, the graph theoretic approach was modified (Figure 33) to accommodate the continuous distribution of habitat suitability scores from the authors' species distribution model of MGS (Saura and Pascual-Hortal 2007). This was accomplished by creating a graph network consisting of "study cells," each with an area of 25 km^2 (Figure 32). The study cells are used to define nodes in the network, which are weighted by summing the suitability scores from the species distribution models (SDM) described in Chapters 2 and 3 (this report). The distance between nodes is estimated using least-cost paths

for each set of eight nearest neighbors, where least-cost paths are calculated using the inverse of the habitat suitability scores from the SDM. Together, the network of nodes and connections

Figure 32: Study area map showing the 1777, 25 km² study cells.
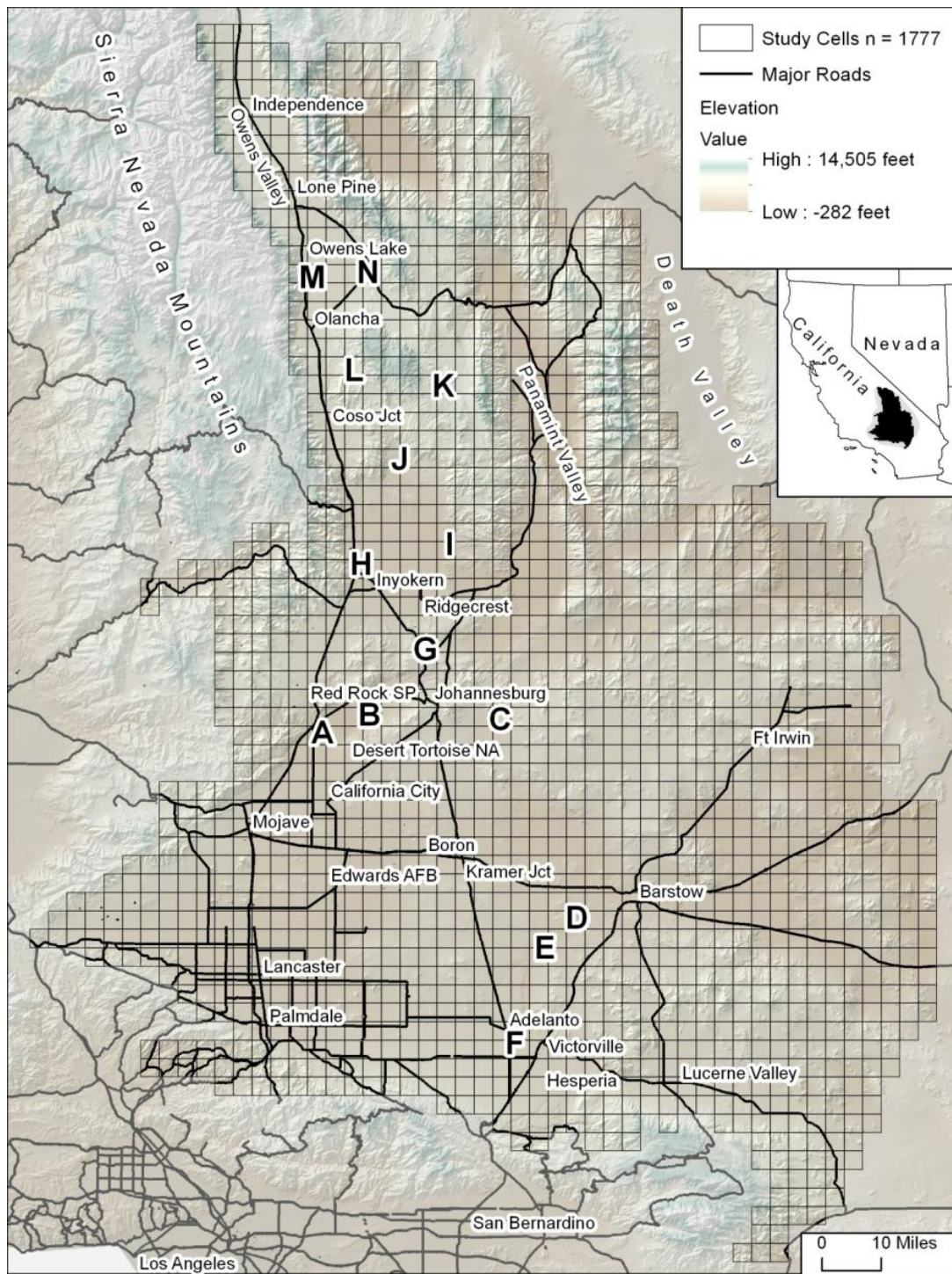
The study cells represent a subset of the study area described in Chapter 2 for habitat modeling. Letters are consistent with those shown in Figure 37.

Figure 33: Flow chart showing the main steps taken for the connectivity analysis. The analysis of climate change corridors using least-cost paths and Circuitscape is not included in this framework but can be viewed as a complimentary analysis using the same resistance maps.

Habitat Model	Expert Opinion
Current climate	*Former Agricultural Lands*
A2 – 2030, 2080	*Exurban Areas*
B1 – 2030, 2080	*Roads*

↓ ↓

Resistance Map ← **Renewable energy**
Calculated as the inverse of habitat suitability — *Wind / Solar / Transmission corridors*

Habitat-Weighted Centroids

↓

Cost-distance
Calculated between habitat-weighted centroids

↓

Conefor ← *Maximum dispersal distance based on maximum inter-generational dispersal*
Graph theoretic software

↓

PCconnector metric

was analyzed using Conefor Sensinode software (version 2.6) (Saura and Torné 2009), which describes the relative importance of nodes for upholding habitat network connectivity. Several metrics are also derived that describe the contiguity or fragmentation of the resulting graph network under climate change, land use, and renewable energy development scenarios.

5.2.2   Study area

The study area, a subset of the one used for the habitat model in Chapter 2 (this report), encompasses the known range of MGS (Zeiner *et al*. 1988-1990). Prior to analyses, the size of the study area was reduced by removing low suitability peripheral areas from the analysis to accommodate software computational limitations. The resulting study area covers 44,425 km^2 and is divided into 25 km^2 (5 km x 5 km) study cells, providing the analysis unit for this study (Figure 32). The 25 km^2 grid was suitable for displaying mapped results because individual cells are readily visible, and because they roughly correspond with the spatial scale at which development might occur. More information about the study area can be found in Chapter 2.

5.2.3   Habitat model

In Chapter 3 (this report) SDMs were used to derive scenarios of potential habitat under various climate change scenarios, and to account for impacts from land use and renewable energy development. Predictions of future MGS habitat under climate change scenarios used the A2 and B1 emissions scenarios published by the Intergovernmental Panel on Climate Change (IPCC) and the Geo-physical Fluid Dynamics Laboratory (GFDL) CM2.1 model (Delworth *et al.* 2006). Chapter 3 (this report) provides more detail on habitat predictions under the two IPCC emissions scenarios. Impacts of land use on MGS habitat were assessed with three land cover types: former agricultural lands and other cleared lands devoid of native shrubs, exurban areas (low density development), and major roads. Habitat suitability scores were reduced in areas where these land use types occurred. Similar to other connectivity efforts (as reviewed in Beier *et al*. 2008) expert opinion was incorporated to assign the magnitude by which habitat suitability was reduced by the land use types that were considered.

Urbanized areas were removed from the analysis by setting the probability of MGS occurrence to zero (Chapter 2, this report). The urban mask was applied to all versions of the habitat model, including current climate, A2 2030, A2 2080, B1 2030, B1 2080, and renewable energy development given the current climate, A2 2030 climate, and A2 2080 climate.

5.2.4   Land use

Habitat suitability scores were reduced in areas largely devoid of vegetation (e.g., playas) because previous work has suggested that such areas represent a significant barrier to juvenile movement (Harris and Leitner 2005). It was assumed that former agricultural and other cleared lands, which are devoid of native shrubs, may function similarly to playas. Habitat suitability values were reduced in these areas as well. Former agricultural lands were digitized from high resolution National Agriculture Imagery Program imagery at a 1:1,500 map scale. These areas were distinguished by a lack of desert shrub vegetation and by the presence of distinct edges in vegetation boundaries, suggesting past agricultural activity.

Exurban areas were identified in a manner similar to how urbanized areas were identified in Chapter 2, except impervious cover values ranging from 12 – 20 percent were used. Primary and secondary roads were extracted from U.S. Census Bureau Topologically Integrated Geographic Encoding and Referencing (TIGER) line files and were augmented with some "secondary highways" as shown on USGS topographic maps (Figure 34).

Figure 34: Lands altered by land-use impacts and potential renewable energy development.
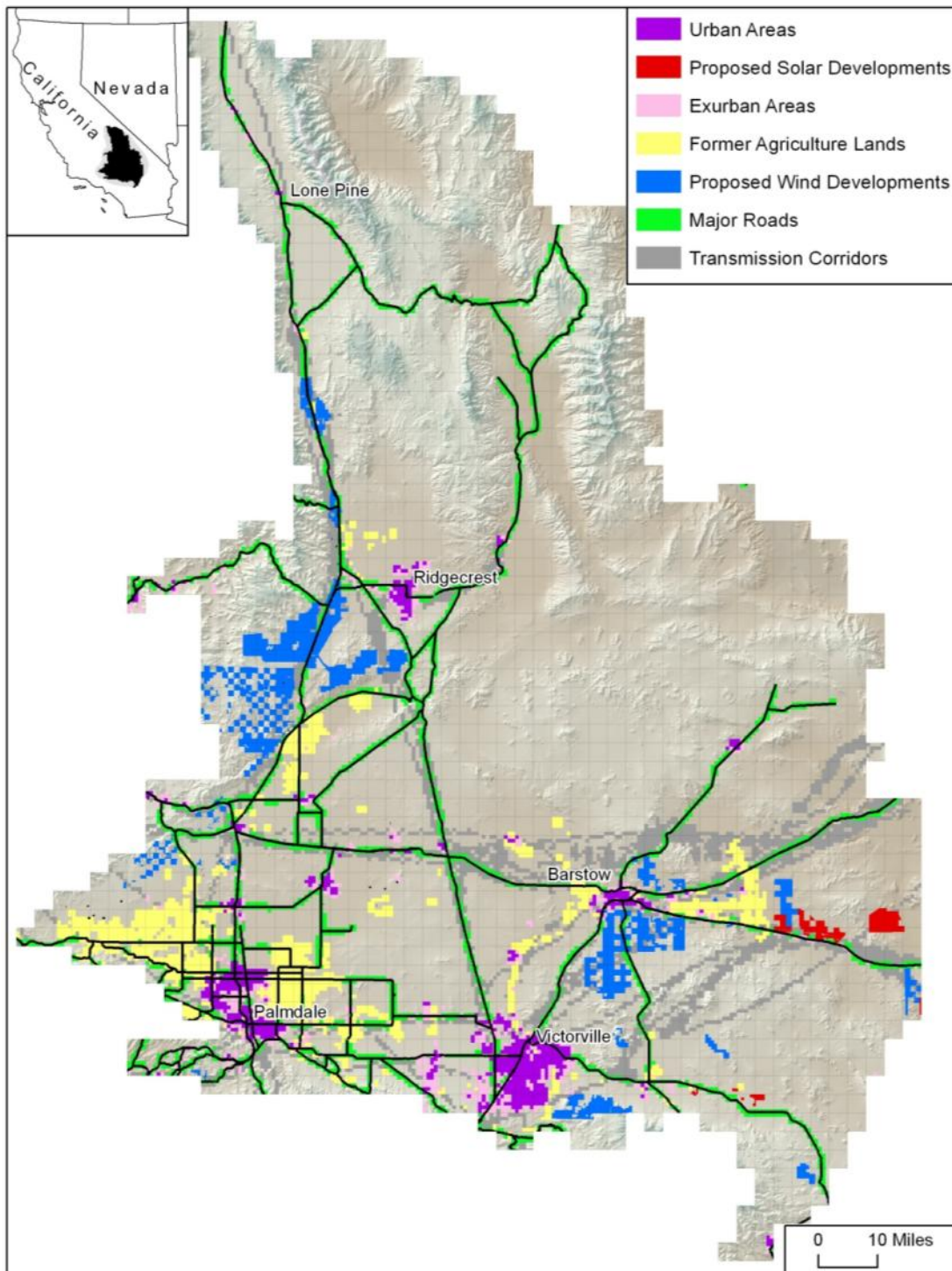
Land uses on the map are arranged based upon their estimated impact on habitat with higher impact land uses being shown on top of lower impact land uses.

The impacts of land use on habitat suitability and movement are not well-understood. Four assumptions of land-use impacts on MGS habitat and resistance to movement, representing assumptions of low, moderate, high, and no impacts were evaluated. In all cases urban areas were reclassified to a value of zero to represent unsuitable habitat. The land use types within each group were combined such that in cells with multiple competing land uses, the maximum reduction value was used to represent probability of occurrence. For example, a cell containing both exurban land use and roads would be decreased 75 percent for the moderate land-use impacts estimation (Table 10). The estimated decrease in MGS probability of occurrence due to land use was then subtracted from the value generated by the habitat model.

Table 10: Estimated increase in resistance to movement due to land-use impacts.

	Former Agriculture	Exurban	Major Roads	Solar	Wind	Transmission
Low	50%	30%	10%			
Moderate	75%	75%	25%	100%	50%	10%
High	100%	100%	40%			

Estimates are derived based on expert opinion. Values represent a percent decrease in the probability of occurrence, which is translated into an increase in movement to resistance. Estimates for renewable energy development were combined with the moderate land-use impacts estimation.

5.2.5 Renewable energy

Expert opinion was employed to assess the potential effects of renewable energy development projects (including transmission corridors, wind energy development areas, and solar energy development areas) on MGS habitat. As described in Chapter 2, spatial representation of current and proposed renewable energy development was compiled for BLM lands in California from the Solar Energy Development Programmatic Environmental Impact Statement (BLM and DOE 2012). Also included were areas designated as transmission corridors under the California Desert Conservation Area Plan of 1980 (BLM 1980), and the West-wide Energy Corridor Programmatic Environmental Impact Statement (DOE and BLM 2008).

The four estimates of land-use impacts were combined with the climate change, and renewable energy development scenarios, resulting in a total of 11 scenarios of predicted habitat (Table 11). Predictions of MGS habitat distributions under the climate change scenarios were reduced by subtracting the decrease associated with the moderate land-use impacts scenario, while predictions of MGS habitat in areas with renewable energy development were reduced by the maximum value in Table 10. For example, a cell with both former agricultural lands and wind energy development is decreased by 75 percent, because the 75 percent associated with former agricultural lands is greater than the 50 percent associated with wind development areas.

Table 11: Matrix showing the model scenarios examined in the connectivity analysis.

	Current climate	A2 2030	A2 2080	B1 2030	B1 2080
None	X				
Low	X				
Moderate	XX	XX	XX	X	X
High	X				

A single X indicates the combination of land use and climate change while a double X indicates the combination of land use, climate change and renewable energy development. In total, 11 models were assessed.

5.2.6 Resistance surfaces and least-cost analysis

Resistance surfaces were derived from the 11 scenarios of predicted habitat by inverting the predictions of habitat (and their associated reductions due to land use or renewable energy development) such that low resistance was found in areas with a high probability of MGS occurrence. The resistance surfaces were then rescaled so that they ranged from a value of 0 for the lowest resistance (highest probability of movement) to 1 for the strongest resistance to movement (and lowest probability of movement). Cost-weighted distances among the habitat-weighted study cell centroids were derived using least-cost analysis (Adriaensen *et al*. 2001). Dijkstra's shortest path algorithm (Dijkstra 1959) was used to determine the optimal (least-cost) route between each study cell centroid and its eight nearest neighbors. For each least cost path, the cost-weighted distance was calculated between the two study cell centroids. This metric is the sum of the cost values along the least-cost path, which represents a cost-weighted distance between two endpoints. Least-cost analyses were conducted using UNICOR software (Landguth *et al*. 2012).

Each study cell contained one habitat-weighted centroid that served as both start and end points in the least-cost analysis. Habitat-weighted centroids were shifted towards higher suitability (1-km^2) habitat cells within the larger (25-km^2) study cell by weighting the geometric mean by the habitat suitability score from the SDM. This habitat-weighted centroid approach provides the flexibility to change position of least-cost start and end points in response to changes in habitat that result from climate change or land use (Figure 35). Habitat-weighted centroids were calculated for each study cell using the mean center tool in ArcGIS 10 with the habitat model representing the weight field (ESRI 2011).

Figure 35: Habitat-weighted centroids derived for four study cells for the no land-use estimation (left) and for the same four study cells with the high land use estimation (right).
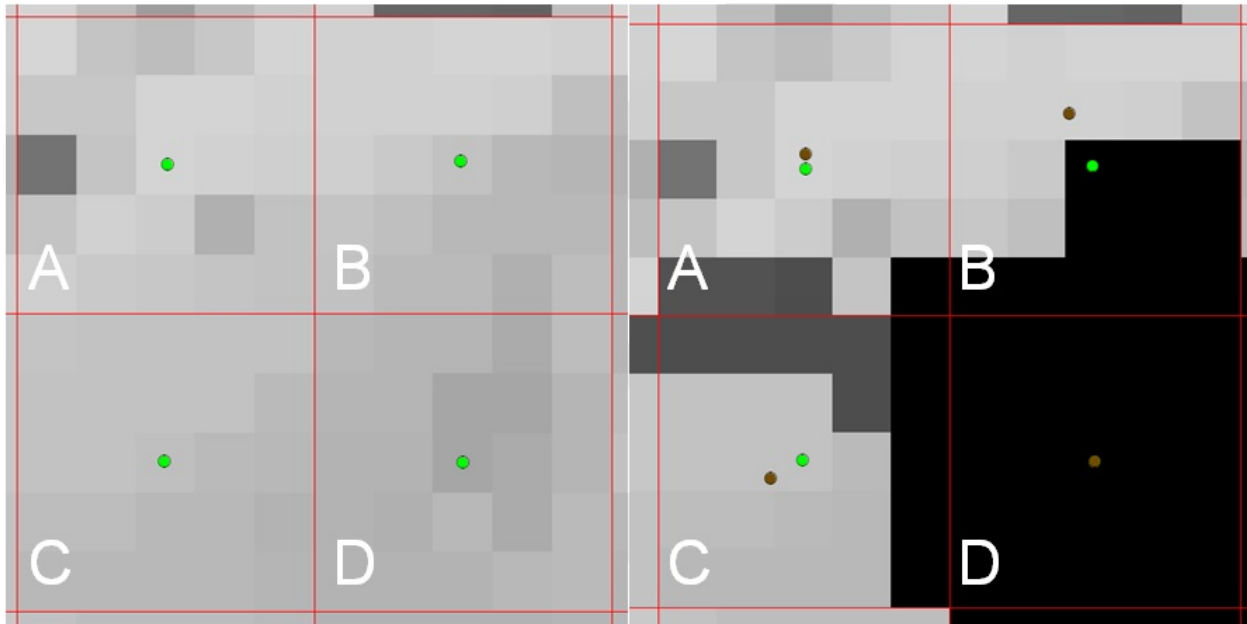
The underlying raster map represents the probability of MGS occurrence with light colors representing high probability of occurrence and dark colors representing low probability of occurrence. Blackened-out squares indicate the presence of land-use impacts. Green dots show the initial habitat-weighted centroids before considering land use and brown dots show the habitat-weighted centroids after considering land use. Prior to considering land use all four study cells have habitat-weighted centroids that do not differ from the geometric centroids (as indicated by the fact that the green dots fall within the center pixel). In study cell A the presence of land use is not sufficient to shift the location of the habitat-weighted centroid beyond the center pixel. In study cells B and C the land-use impacts shift the habitat-weighted centroids to the northwest and southwest respectively. In study cell D the land-use impacts affect all pixels equally, therefore not shifting the location of the habitat-weighted centroid.

5.2.7 Connectivity and graph theory

Radio-tracking of juvenile MGS indicates that the average dispersal distance is 1.5 km for males and females with a range from 0 to 3.9 km (Harris and Leitner 2005). This generally exceeds the range that adult squirrels moved (Harris and Leitner 2005). Thus long-distance dispersal of juveniles is considered crucial for connecting populations and for serving to recolonize areas subject to extinction. However, the resolution of both the habitat model and the 5x5 km study cells used to assess connectivity were far too coarse to allow for simulation of movement of individual squirrels. Species that require multiple generations to move between protected habitat blocks have been referred to as corridor dwelling species (Beier *et al*. 2008). Due to the multi-generational nature of dispersal these species require suitable habitat within the movement corridor. In this analysis MGS was characterized as a corridor dwelling species due to the continuous nature of its habitat (Chapter 2, this report) and the long distances between protected habitat areas. Movement between study cells was assessed as multi-generational movement.

A previously developed framework (Saura and Rubio 2010) was used for simultaneously assessing the value of a study cell in terms of its habitat suitability and its position within the habitat network. This approach recognizes that a study cell may serve one or more of three functions: (1) contain habitat suitable for occupation by the target species that is valuable even in the absence of connectivity to other cells; (2) produce a flux of emigrants that can colonize other study cells; and (3) serve as a "stepping stone" that facilitates movement between other cells because of its position within the network. All three measures can be described using the PC (probability of connection) index (Table 9), which was calculated using Conefor software (www.conefor.org).

The PC index describes the importance of patches in upholding network connectivity (Table 9). The PC index assesses connectivity by iteratively removing patches and re-calculating the likelihood that two randomly placed animals can reach one another given the habitat configuration. The PC index can be parsed into three fractions – intra, flux, and connector. The intra fraction describes the habitat value in the absence of connectivity with other cells. The flux fraction quantifies the role that a cell may play in providing fluxes of migrants to other cells. The flux fraction is influenced by both habitat quality of the cell and the number of quality connections to other cells. The connector fraction (PCconnector index) describes the importance of a patch for facilitating movement through the patch to access other patches. Patches with a high value are more important for upholding connectivity because their position within the network is central and their redundancy is relatively low. Patch and node redundancy (having multiple potential movement paths) has been shown to be important properties, because the removal of one of these cells may have a larger-than-average impact on overall connectivity (Baranyi *et al*. 2011).

Conefor software requires a node file, a link file, and an estimation of dispersal probability. For the node file the habitat-weighted centroids were used with weights derived by summing all habitat values within each 5x5 km study cell. The link file was derived as the cost-weighted distance between habitat-weighted centroids from the previous UNICOR analysis. Individual dispersal distance was not used due to the relatively continuous nature of MGS habitat (Chapter 2, this report). Habitat graphs were constructed by connecting each habitat-weighted centroid with the eight neighboring study cells representing link strength with the cost-weighted distance (Figure 36). Known occurrences of MGS were then plotted on the habitat graph and the minimum value required to connect 95 percent of known occurrences was used to determine the maximum dispersal distance in cost-distance units. The rationale was that connectivity must have been sufficient to allow movement to known occupied sites. Negative exponential decay function was fitted to determine the 50th percentile in cost distance units. This value was subsequently used for all analyses involving Conefor software. This approach addresses the problem of "corridor dweller" species for which long-range dispersal is inter-generational.

Figure 36: The minimum spanning tree approach to defining maximum dispersal distance.
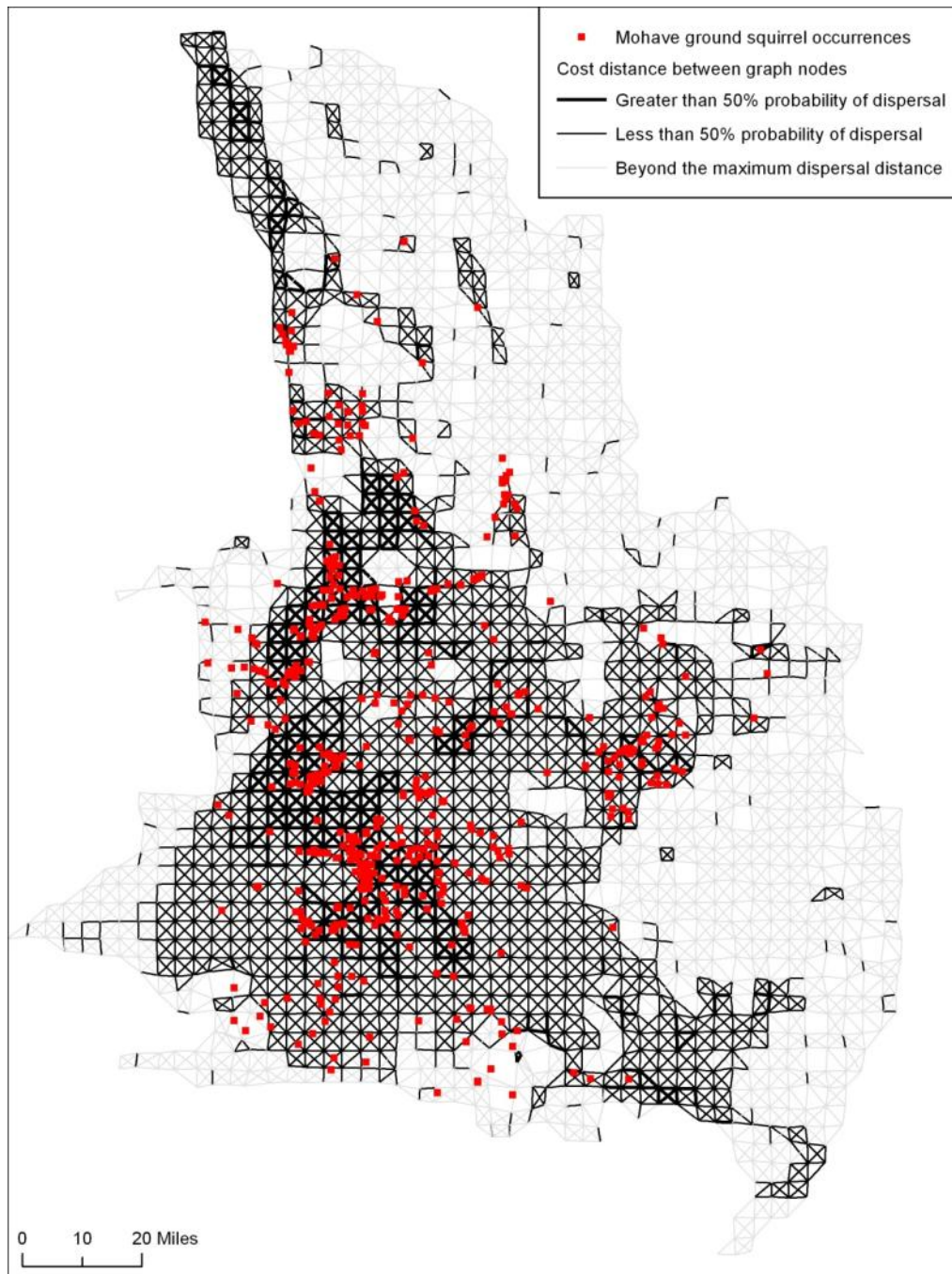
Only links less than 8000 meters (Euclidean distance) were used to generate the graph. Links colored gray are not available to dispersers due to high movement costs. Outlying components of the graph may be below the required cost threshold but are not accessible based on the location of known points of occurrence. Bold links are highly connected while moderately bold links are moderately connected. This approach is designed to estimate inter-generational dispersal, not individual dispersal.

In addition to using graph theory to derive metrics of connectivity for individual nodes (study cells) several metrics were derived to describe the entire graph. This allows for direct comparisons among climate change scenarios and land use impact estimations. The following metrics were derived for all 11 graphs: amount of habitat available, total length of all graph links, length of all links making up the largest graph component, PC numerator, and equivalent connected area index (EC_{PC}; Table 9). The PC numerator serves as an indication of the overall level of connectivity within the network (Saura and Pascual-Hortal 2007) while the EC_{PC} indicates the equivalent amount of habitat if the habitat consisted of a single patch (Saura *et al*. 2011). The EC_{PC} index is particularly useful because changes that result in the loss of habitat that is above average in upholding connectivity will result in a larger decrease in EC_{PC} relative to the decrease associated with habitat loss.

5.2.8 Analysis of movement corridors to accommodate climate change

To assess the impact of landscape resistance on the ability of MGS to shift in response to climate change, least-cost and Circuitscape analyses were performed on the northern portion of the MGS range. While least-cost paths indicated the optimal route between source and destination points, Circuitscape analysis (McRae 2006) simultaneously assesses all potential pathways of movement between source and destination points. Maps produced from Circuitscape analysis are useful for identifying alternative routes of movement as well as identifying critical "pinch points" that may impede movement (McRae *et al*. 2008). Two such areas, predicted to be important for genetic diversity in future climate scenarios, were selected for these analyses. In addition to those areas, Circuitscape analysis was performed on the current MGS range using current habitat conditions and known MGS occurrence points. The first critical area facilitated range expansion northward to areas of suitable climate over the next century. Future-climate scenarios suggest that MGS will need to expand its range from the present northernmost occurrences near Olancha northward to areas in Owens Valley near the town of Independence (by the year 2080). The second critical area connects the mid-western/central population with the northern population. Movement of MGS through this zone is critical for supporting sufficient population numbers and genetic diversity needed to facilitate range expansion.

For the analysis of landscape connectivity given current conditions, known occurrence points were used as the source cells in the Circuitscape analysis (Chapter 2, this report). Circuitscape analysis was performed in pairwise fashion by calculating the cumulative current between pairs of points (Shah and McRae 2008) using the inverse of the current conditions habitat model as a map of resistance. The resulting map was interpreted visually to identify bottlenecks in movement and was compared to outputs from graph theoretic methods.

A location on the edge of Owens Lake was selected as the source point for the range expansion analysis, while a location 16 miles north of the town of Independence, at the edge of the habitat model study area, was selected as the destination point. The A2 resistance raster for year 2030 was used to determine cost distance from the Owens Lake location and a least-cost path was mapped using the Spatial Analyst extension in ArcGIS (ESRI 2011). Least-cost analysis results in a path of least resistance that is a single cell wide. Reliance upon such a narrow corridor for conservation planning purposes can be impractical and misguided; therefore most corridor

designs are greater than a single cell in width (Beier *et al*. 2008). One cost-distance raster used the point at Owens Lake as the source cell, while the other raster used the point north of Independence as the source. The two cost-distance rasters were then added together. Cells were grouped into two categories: less than the critical threshold needed to make a continuous corridor and greater than the threshold required to make a continuous corridor. Then the same source and destination points and resistance map were used to construct cumulative resistance (Table 9) maps with Circuitscape software limiting the analysis to the potential movement corridor for range expansion (Shah and McRae 2008).

A similar analysis was performed on the second critical area connecting the central population with the northern population. Six source points were located within the central portion of the MSG range, as defined by Bell and Matocq (2011), all in areas with a high probability of MGS occurrence. The destination point was the location at Owens Lake used in the range expansion analysis as the source cell. As with the range expansion analysis, movement corridors were created using cost-distance rasters with a threshold of 20,000 cost-distance units. In addition, this analysis used both the present-day and the A2 2030 climate scenario resistance rasters to provide a comparison of how climate change might affect the location of the movement corridors. A least-cost analysis was performed to determine optimal paths from each of the six sources to the single destination for current climate and A2 2030, resulting in 12 least-cost paths. Circuitscape analyses were conducted for current climate and A2 2030 climate using the same resistance rasters as in previous steps, but limiting the analysis to the area contained within the movement corridors.

5.3 Results and Discussion

5.3.1 Current critical areas for connectivity

The importance of habitat corridors and structure of landscape connectivity depends very much on the arrangement of suitable habitat across the species range, particularly given the modeling approach. The habitat model shows a highly clustered pattern, with suitable habitat extending fairly continuously across much of the reported range, from Palmdale in the south, north past Ridgecrest including China Lake, and east to Fort Irwin (Figure 37a). More discrete patches of highly suitable habitat, isolated from the rest, are predicted to occur from Olancha to the Owens Valley north of Lone Pine, slightly outside the current known distribution of the species, and east of Victorville. Although there is a large aggregation of highly suitable habitat in these areas, a smaller subset has a disproportionately important role in facilitating connectivity among suitable habitat patches (Figure 37a and 37b). The habitat graph indicated at least 14 areas that were deemed "important connectivity areas" (Figure 37). These include the more important graph links and nodes that serve as vital connectors linking more isolated habitat clusters with larger core areas. Important connectivity areas were located throughout the MGS range and included locations such as Fremont Valley (A), Cuddleback Lake (C), the areas south, west, and east of Ridgecrest (G, H, I), Coso Basin (J), and Cactus Flat (L), among others (Table 12, Figure 32). Areas with study cells that have large PCconnector values were identified, and hence are located centrally while having low redundancy (i.e., their connective function cannot be replaced by other high-connectivity patches). Several important connectivity areas, including

Figure 37: Present-day Mohave ground squirrel habitat availability and connectivity based on the moderate land-use impacts estimation.
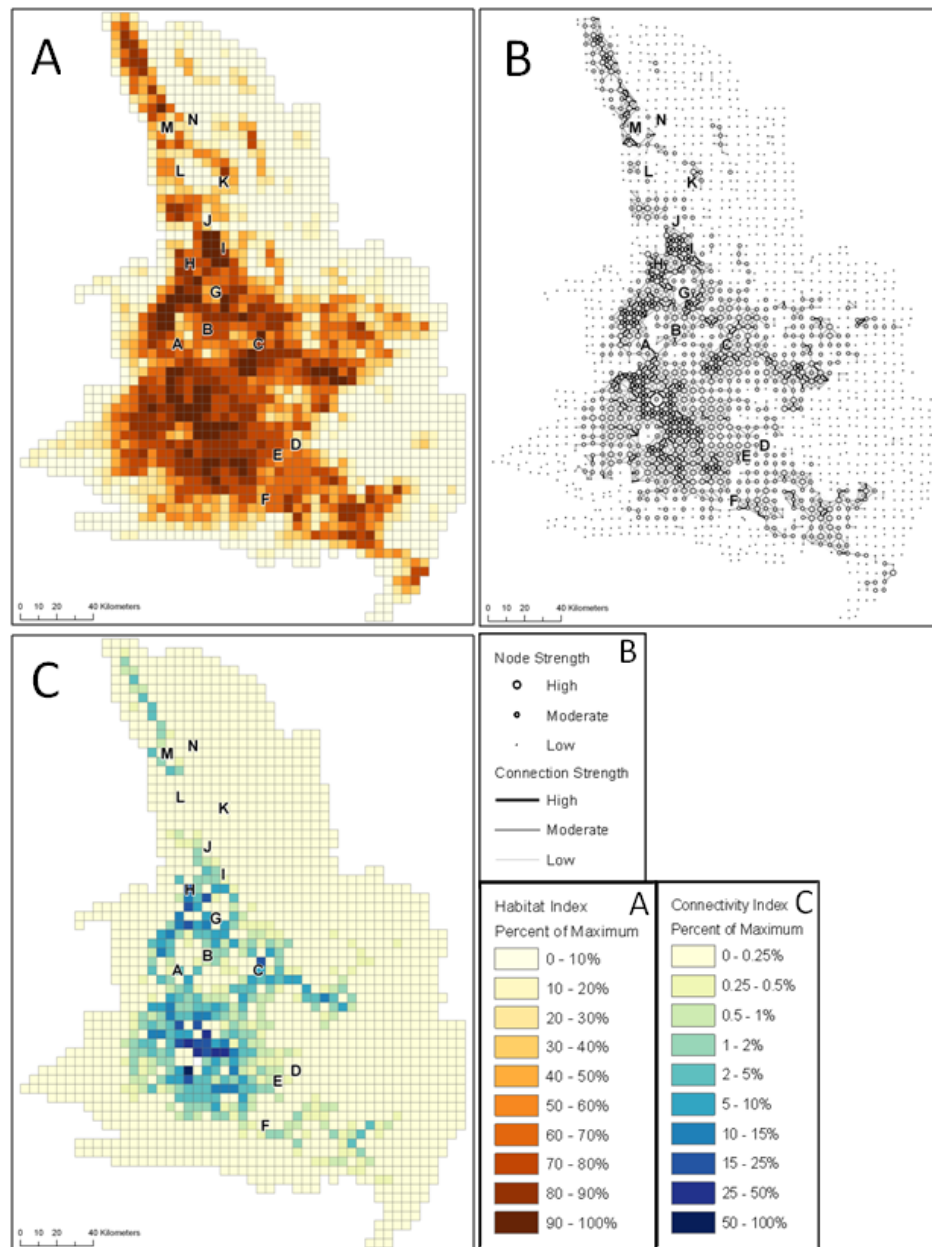
A) Habitat availability is expressed as a percentage of the maximum possible value derived from MGS probability of occurrence modeling. A value of 100% indicates that within a 5 km grid cell, all 1 km raster grid cells have the maximum habitat value. B) Graph view of the habitat network with the size of circles indicating node strength and the width and tone of lines indicating connection strength. Node strength was calculated based on the total available habitat within the 25 km^2 grid cells. Link strength was calculated based on the cost-weighted distance between the habitat-weighted centroids of the 25 km^2 grid cells. The position of nodes within the network is not perfectly gridded because the position of the habitat-weighted centroids was allowed to vary based upon the availability of habitat. C) The connector component of the probability of connection index (PCconnector, Saura and Rubio 2010) indicating the importance of the position of the 25 km^2 grid cell within the overall habitat network. Cells with a high value are more important for upholding connectivity because their position within the network is central and their redundancy is relatively low (Baranyi et al. 2011). The removal of one of these cells would have a larger-than-average impact on overall connectivity.

Table 12: Important connectivity analysis areas identified from the habitat graph, evaluated as strong or weak connections using the connectivity index (PCconnector), and evaluated as strong or weak connections in the Circuitscape analysis.

Map Label	Important connectivity areas	PCconnector	Circuitscape
A	Fremont Valley	Y (weak)	Y (strong)
B	Summit Range	Y (weak)	Y (weak)
C	Cuddleback Lake	Y (strong)	Y (weak)
D	Calico Mountains	N	N
E	Johnsons Corner	N	N
F	Mojave Heights/Adelanto	N	Y (strong)
G	south of Ridgecrest	Y (strongest)	Y (strong)
H	Indian Wells	Y (strong)	Y (strong)
I	China Lake	Y (strong)	Y (strong)
J	Coso Basin	Y (weak)	Y (strongest)
K	Coles Flat	N	Y (weak)
L	Cactus Flat	N	Y (weak)
M	west of Owens Lake	Y (weak)	N
N	east of Owens Lake	N	N

Fremont Valley, areas around Ridgecrest, and Cuddleback Lake exhibit large PCconnector values while other areas, such as Calico Mountains (D), Johnsons Corner (E), Mojave Heights (F), Coles Flat (K), Cactus Flat (L), and Owens Lake (M, N) have very small PCconnector values. In addition there are some areas that have large PCconnector values such as Edwards Air Force Base that were not visually detectable as important connectivity areas on the habitat graph (Figure 37b).

Several factors may have contributed to the discrepancy between visual detection of important corridors from graph analysis, and quantitative ranking of the study cells using the PCconnector index. First, the PCconnector index is derived from nodes and links that are weighted based upon their habitat value and their cost-weighted distance from one another. Corridors located at the periphery of MGS range may not be central enough to support large outward dispersal fluxes of squirrels. However, they may facilitate range shifts in response to climate change or other factors, particularly if they are located in a section of MGS range that is expanding in response to climate change. Baranyi *et al*. (2011) found that the prerequisites for a high PCconnector value include a high 'betweenness' centrality and a low redundancy. Therefore peripheral study cells may receive lower values of PCconnector because they have low 'betweenness' currently; however, with future climate change scenarios the PCconnector value could increase. Second, simulations by Rubio and Saura (2012) show that the particular combination of low overall habitat area with relatively high fragmentation, coupled with a species with relatively small dispersal ability, increases the likelihood that the PCconnector index will be of high overall value. They compare these simulation results with three real

species: capercaillie (*Tetrao urogallus*), Tengmalm's owl (*Aegolius funereus*), and the black woodpecker (*Dryocopus martius*), which had overall PCconnector fractions (PCconnector / overall PC) of 30 percent, less than 10 percent, and 15 percent respectively. The results for MGS had a PCconnector fraction of 18 percent indicates that MGS may be one species that can benefit from corridor conservation strategies. Furthermore the distribution of high PCconnector fractions varied throughout the range of MGS habitat with 0.4 percent of study cells having PCconnector fractions greater than 50 percent and 4 percent having PCconnector fractions greater than 25 percent.

The two study cells with the highest connectivity values (PCconnector statistic) were located within Edwards Air Force Base adjacent to Rogers Dry Lake. Although not clearly visible on the habitat graph, Rogers Dry Lake likely serves as a significant barrier that MGS must navigate around.

Circuitscape analysis augments the graph analysis by providing an alternative view of connectivity at a finer scale. Areas of greater current from Circuitscape analysis indicated either a high potential for MGS movement due to the proximity to known occurrences, or areas where movement is constricted or funneled due to limited habitat availability, known as bottlenecks or pinchpoints (Rudnick *et al*. 2012). The latter were interpreted as areas that may be important for maintaining connectivity for MGS. It was found that the Coso Basin was one area of exceptionally strong current (Area J on the map in Figure 38). The area is the current "gateway" to the northern MGS populations. In addition to this area of exceptionally high connectivity there was evidence for other areas playing an important role in providing connectivity. Areas A, B, C, F, G, H, I, K, and L (Table 12; Figure 38) all appeared to exhibit increased current compared to surrounding cells on the map while Areas D, E, M, and N all showed relatively little current. The lack of current in these latter areas may be due primarily to the peripheral locations of those areas and the lack of populations to serve as sources of dispersers.

Figure 38: Map of cumulative current derived from the Circuitscape analysis.
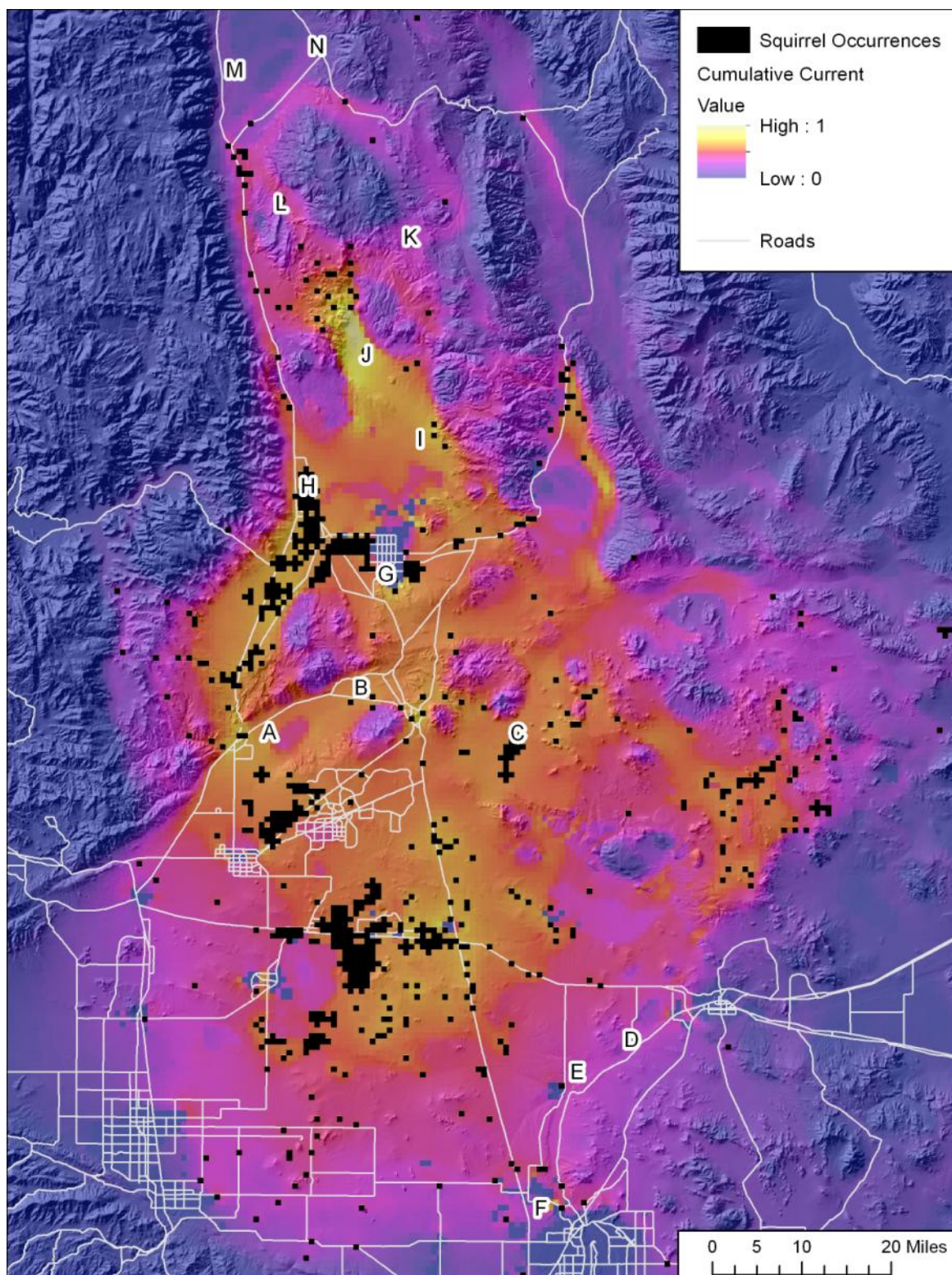
Sources are shown as black cells on the map and represent locations of known MGS occurrence. Areas portrayed by warmer colors indicate high current either because they are close to source cells or because they represent areas where movement is constrained by habitat (e.g., area J on the map).

Ninety-six percent of MGS habitat is within the largest graph component suggesting that movement is likely among the core habitat areas (Table 13). However, that result is based on the maximum intergenerational dispersal distance, which is a parameter that cannot be validated. Several portions of the overall MGS population appear to be somewhat disconnected or to rely on relatively narrow corridors of suitable habitat for dispersal (Figure 37b). The major regions of high-suitability habitat that are relatively disconnected in the graph network roughly correspond to the three genetically distinct groups described by Bell and Matocq (2011), including a Northern population (Olancha, Cactus Peak, Coso Basin), a Mid-western/Central population (Freeman Gulch, El Paso Mountains), and a Southern population (DTNA east to Fort Irwin). Bell and Matocq (2011) (also referenced in Chapter 4 of this report) found greater genetic admixture in the mid-western central region. Their findings correspond with results reported here in that the southern region has the most continuous habitat, there is opportunity for connectivity between the southern and mid-western/central region, and the northern region is most isolated.

Table 13: Graph metrics for each land use impact estimation.

	None	Low	Moderate	High
Total Graph Length	19,418.48	18,510.89	17,714.00	16,994.20
Length of Largest Component	18,689.36	17,717.89	16,996.00	16,135.89
Proportion of Largest Component	0.96	0.96	0.96	0.95
Habitat Area	10,695.09	9,971.24	9,534.09	9,266.70
PC numerator	1,579,695.00	966,398.00	914,171.8	762,699.30
EC_{PC} index	1,256.86	983.06	956.12	873.33

5.3.2 Effects of current land-use on MGS landscape connectivity

Recent and historical land-use practices have reduced the amount of habitat and degree of habitat connectivity for MGS (Figures 39 and 40). The moderate land-use classification reduced habitat area by 11 percent relative to a classification that considers only land-use impacts of urban areas, but not the effects of roads, agriculture and other land-use types (Table 13). However, a 32 percent reduction in EC_{PC} index (Table 13) greatly exceeds the relative reduction in habitat area, indicating that the habitat lost through land-use development is disproportionately important to MGS connectivity. This is likely due to the diffuse distribution of road networks and other human developments. Despite the widespread effects of roads and other human developments, 95 percent of the overall graph remains composed of a single component (Table 13), suggesting that a diminished level of movement is possible, but that critical populations are not likely to become completely genetically isolated as would occur if the graph fractured into multiple components. There are several important exceptions to this,

however. Many of the former agricultural lands and exurban areas in the southern and southwestern portion of the range near Palmdale have severely diminished MGS habitat (Figure 39), but have had relatively minor impacts on MGS connectivity (Figure 9) because they exist at the southern periphery of MGS range. Former agricultural areas and roads appear to have diminished the functionality of important corridors connecting Fremont Valley with Freeman Gulch (Figure 40 indicated by an "A" on the map). This area historically may have been among the most important areas for connecting the Mid-western/central and southern populations as identified by Bell and Matocq (2011). For the relatively highly developed Ridgecrest area, connectivity is even further reduced for the high-impact, urban land-use classification. Otherwise, there is little difference among land-use classifications with respect to predicted patterns of landscape connectivity. Given the relatively small differences among land-use classification assumptions, subsequent analyses are reported only for the moderate land-use classification.

Figure 39: Difference in habitat availability with different land-use impacts estimations.
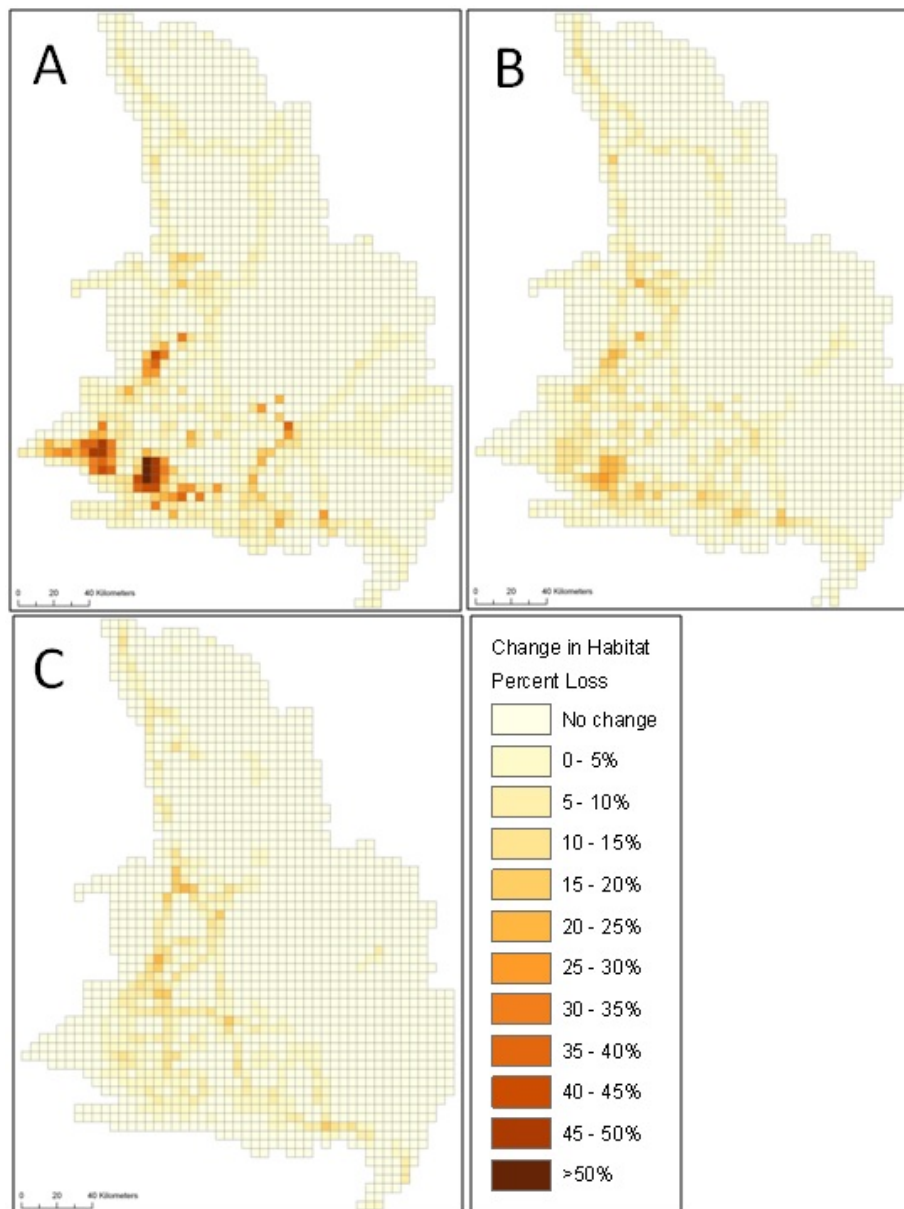
A) Difference between the "urban only" impacts estimation and the low land-use impacts estimation. B) Difference between the low land-use impacts estimation and the moderate land-use impacts estimation. C) Difference between the moderate land-use impacts estimation and the high land-use impacts estimation.

Figure 40: Land-use impacts on Mohave ground squirrel habitat connectivity as measured by the connector component of the probability of connection index (varPCconnector; Saura and Rubio 2010).
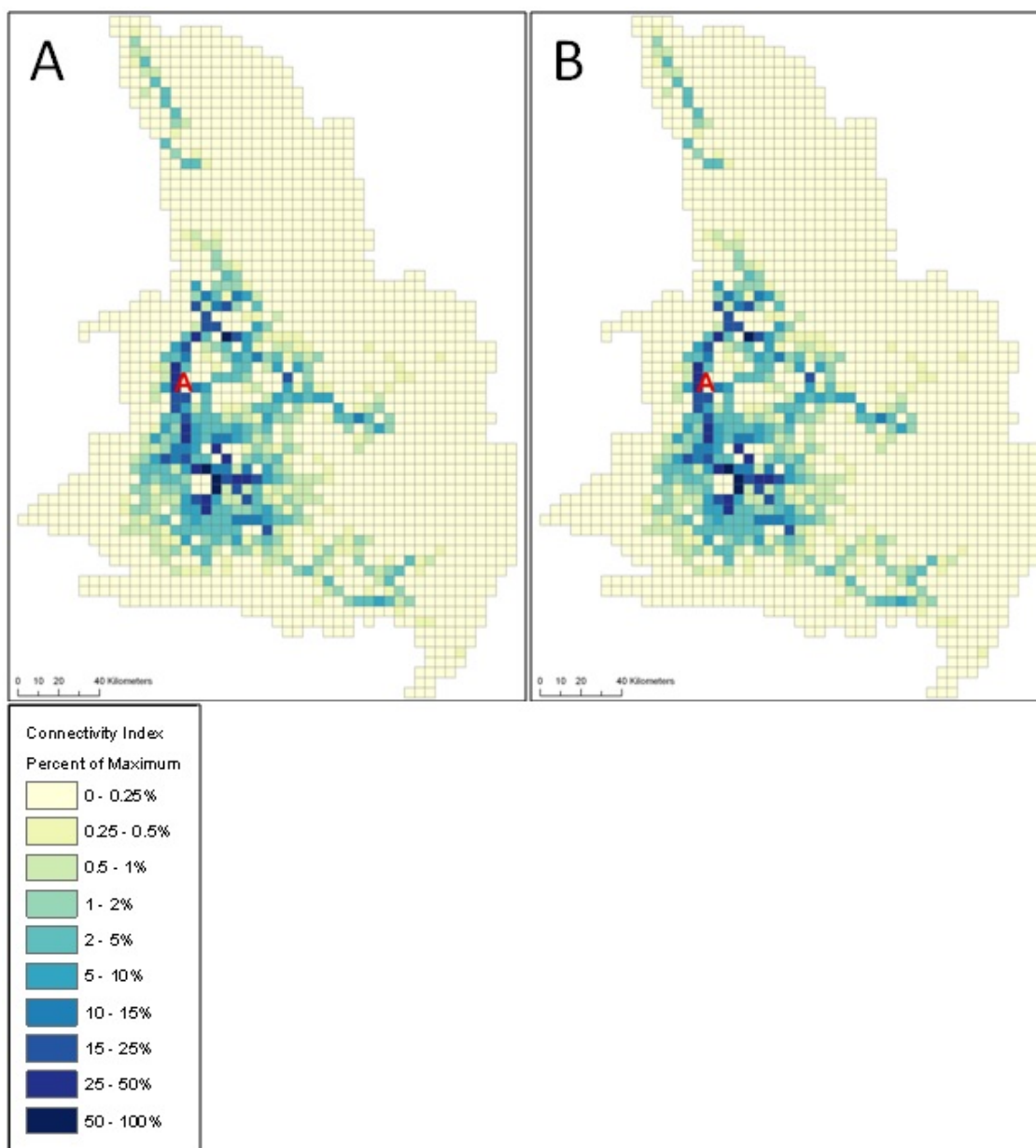
Values are expressed as a percentage of the highest value in the landscape (varPCconnector = 30,000). A) Habitat connectivity using a habitat model that only includes the land-use impacts of urbanized areas. Habitat availability in urban areas is reduced by 100%. B) Habitat connectivity using a habitat model based on moderate estimates of land use that include a reduction in former agriculture land and land with cleared vegetation by 75%, exurban areas by 75%, major roads by 25%, and urban areas by 100%. "A" on the map indicates a former connection between Freeman Gulch and Fremont Valley that is now greatly diminished due to the presence abandoned agricultural fields.

Figure 41: Climate change impacts on Mohave ground squirrel habitat using climate change scenarios combined with the moderate land-use impacts estimation.
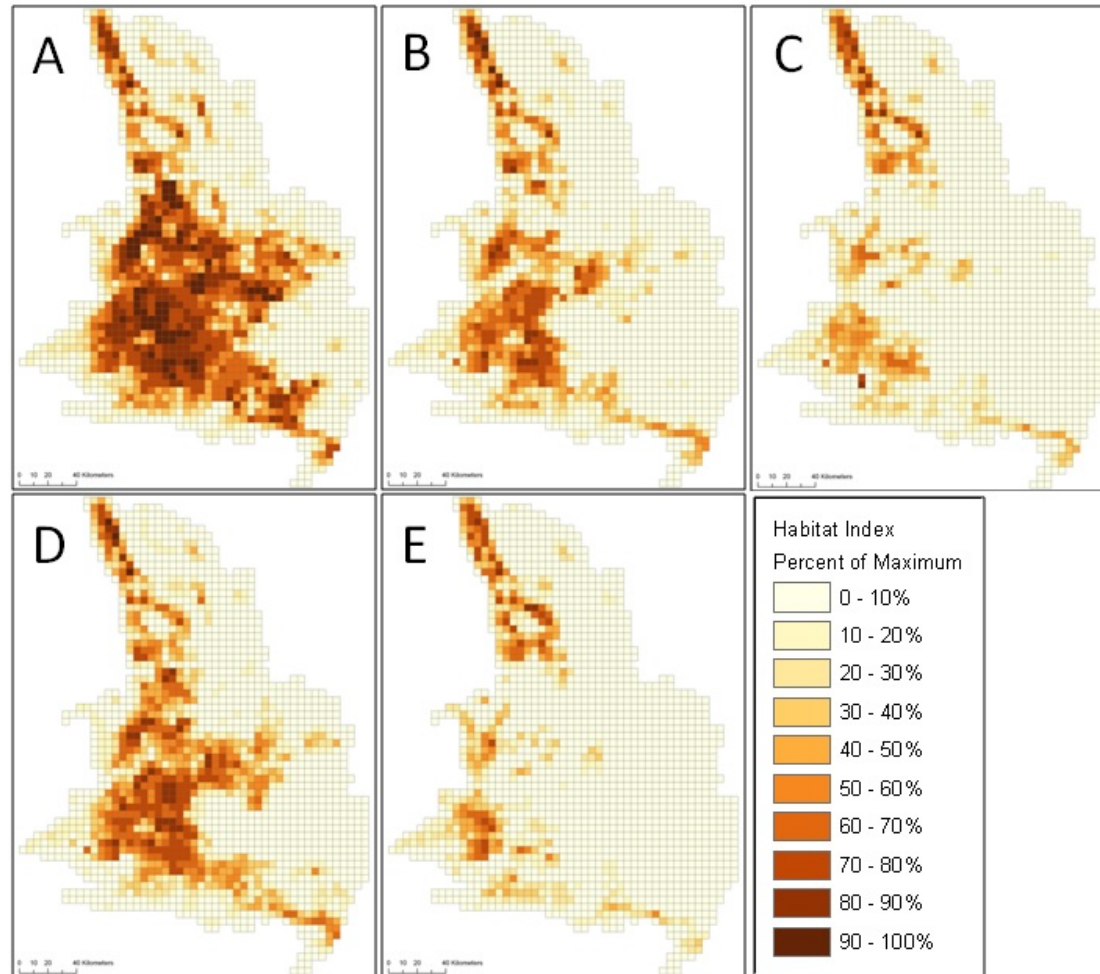
A) Current habitat suitability with moderate land-use impacts. B) Habitat suitability in 2030 assuming the A2 emissions scenario. C) Habitat suitability in 2080 assuming the A2 emissions scenario. D) Habitat suitability in 2030 assuming the B1 emissions scenario. E) Habitat suitability in 2080 assuming the B1 emissions scenario.

5.3.3 Climate change effects

Potential impacts of climate change appear to exceed past and current impacts of urban development, agriculture, and roads with respect to both area of MGS habitat and overall landscape connectivity. Predictions derived from both A2 and B1 scenarios converge on similar habitat maps by 2080 (Figure 40), leading to forecasts of future MGS habitat and connectivity that are greatly reduced relative to today. The predicted habitat model for the A2 scenario in the year 2080 shows a 66 percent loss of habitat area and corresponding reductions in total graph length, length of largest component, and EC_{PC} index of 72 percent, 88 percent, and 73 percent, respectively (Table 13).

Climate change predictions result in dramatic fragmentation of currently suitable habitat areas. Habitat becomes unfavorable by 2080 in all of the current range except for the northern (Owens Valley) area and novel habitats at higher elevations in the Coso Range as well as the flank of the Sierra Nevada Mountains (Figure 41). Areas of high functional connectivity, given future climate change scenarios, are similarly located to the north, west, and south of the current MGS Range (Figures 42 and 43). Future habitat predictions include marginal MGS habitat in the central and southern portions of the range that are predicted to have very low connectivity within and between habitat clusters (Figures 42 and 43). These include the area to the west of Red Rock Canyon State Park and the area bounded by Mojave, Lancaster, and Edwards Air Force Base (Figure 32). Both areas are at the western margin of the currently reported MGS range. Only the northernmost portion of the potential range from Olancha north through Owens Lake, into Owens Valley, and newly-available habitat in the Coso Range is predicted to retain high connectivity (Figures 42 and 43).

Figure 42: Graph view of climate change impacts on Mohave ground squirrel connectivity using climate change scenarios combined with the moderate land-use impacts estimation.
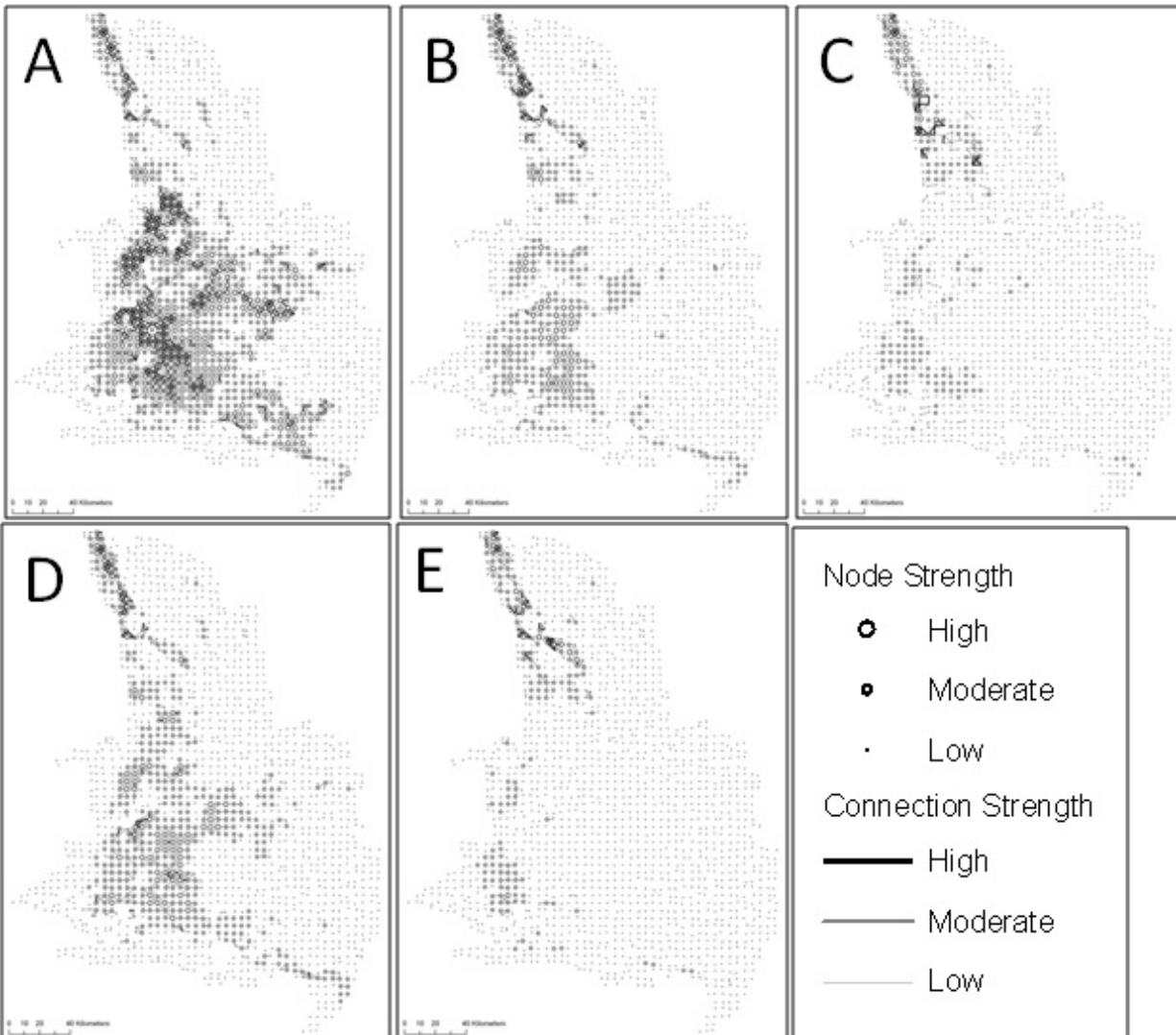

A) Current connectivity with moderate land-use impacts B) Connectivity in 2030 assuming the A2 emissions scenario. C) Connectivity in 2080 assuming the A2 emissions scenario. D) Connectivity in 2030 assuming the B1 emissions scenario. E) Connectivity in 2080 assuming the B1 emissions scenario.

Compared with the estimation of land-use impacts, climate change appears to have a much greater influence on the amount of MGS habitat available (Figure 44). Between 2010 and 2030 there is a 45 percent habitat loss under the A2 scenario and a 33 percent habitat loss under the B1 scenario. Between 2030 and 2080 estimated losses are 38 percent and 53 percent for the A2 and B1 scenarios, respectively (Table 14). Habitat loss due to climate change appears to fracture the graph into multiple components with the three largest components roughly corresponding with the three populations identified in Bell and Matocq (2011) (Figure 42). However, as measured by Euclidian Distance (rather than cost-weighted distance), the timing of the habitat graph fragmentation differs between climate change scenarios with the B1 scenario providing a more connected graph in 2030 compared to the A2 scenario (Figure 45). Ultimately both

scenarios point to a highly fragmented graph that would severely impede gene flow between the southern, central, and northern regions.

Figure 43: Connectivity index under different climate change scenarios using climate change scenarios combined with the moderate land-use impacts estimation.
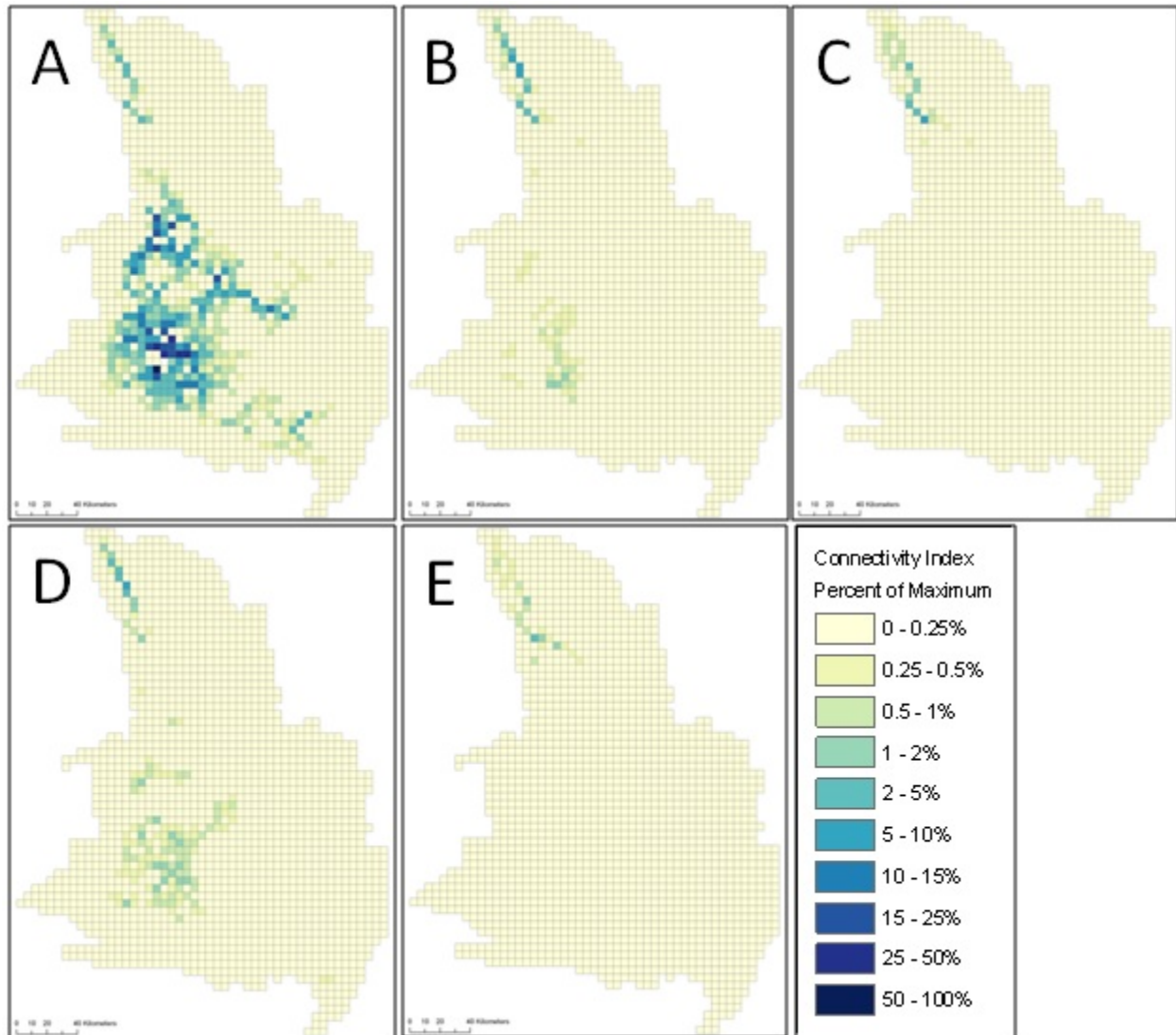
A) Current connectivity in the absence of land-use impacts B) Connectivity in 2030 assuming the A2 emissions scenario. C) Connectivity in 2080 assuming the A2 emissions scenario. D) Connectivity in 2030 assuming the B1 emissions scenario. E) Connectivity in 2080 assuming the B1 emissions scenario.

Figure 44: Amount of available habitat weighted by habitat suitability (sum of raw SDM values) for each climate change scenario only and each climate change scenario in combination with the moderate land use estimation.
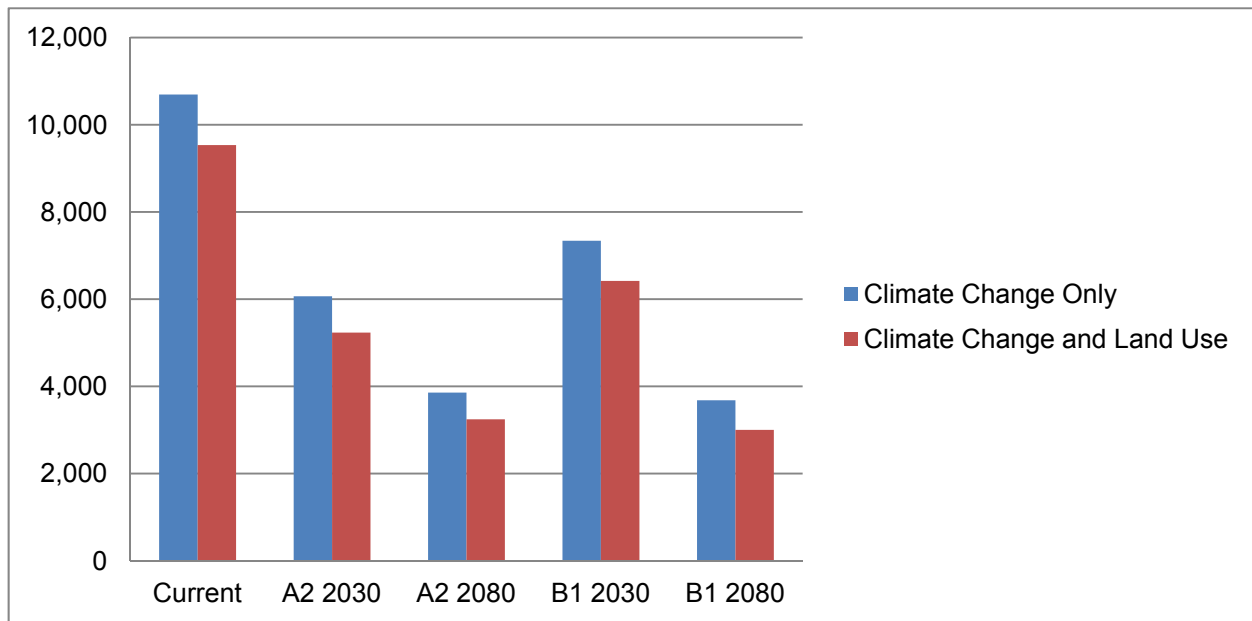
Figure 45: Total link length for the entire graph and total link length for the largest graph component.
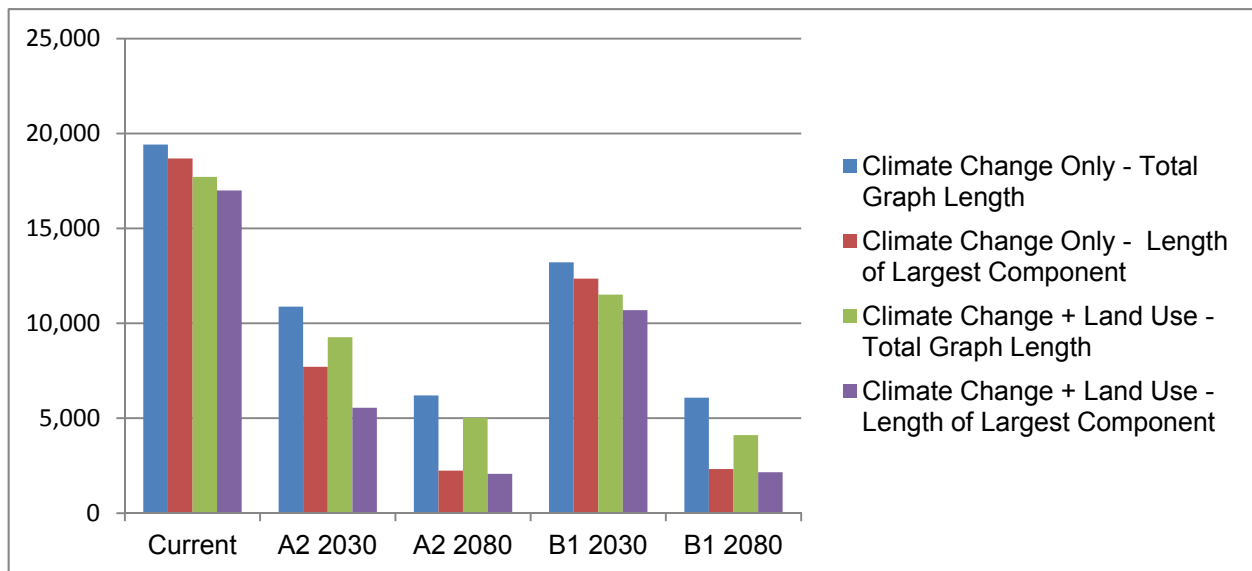
Table 14: Graph metrics for climate change scenarios with moderate land-use impacts estimation.

	Current/ moderate land use	A2 2030	A2 2080	B1 2030	B1 2080
Total Graph Length	17,714.00	9,269.16	5,018.44	11,513.52	4,113.82
Length of Largest Component	16,996.00	5,555.03	2,073.94	10,694.01	2,158.59
Proportion of Largest Component	0.96	0.60	0.41	0.93	0.52
Habitat Area	9,534.09	5,233.92	3,245.05	6,417.23	3,003.41
PC numerator	914,171.8	137,086.50	53,163.65	187,597.30	126,020.10
EC_{PC} index	956.12	370.25	230.57	433.13	354.99

5.3.4 Modeling corridors important for climate change response

Climate change analyses indicate that, while the majority of areas are predicted to experience range contraction, a few areas are predicted to see MGS range expansion. Owens Valley north of Olancha is one area in particular where latitudinal range expansion is expected (Chapter 3, this report). The movement corridor for range expansion in Owens Valley encompasses the vast majority of the valley floor and some foothills (Figure 46). The most likely least-cost route of movement travels around the west side of Owens Lake and up the east side of Owens Valley. Alternative less preferred routes traverse the east side of the lake (i.e., southwest of the labeled pinch points) as well as the more gradual foot slopes of the Sierra Nevada (i.e., west of B in Figure 46).

Figure 46: Least-cost path and cumulative current for future MGS range expansion in the southern Owens River Valley.
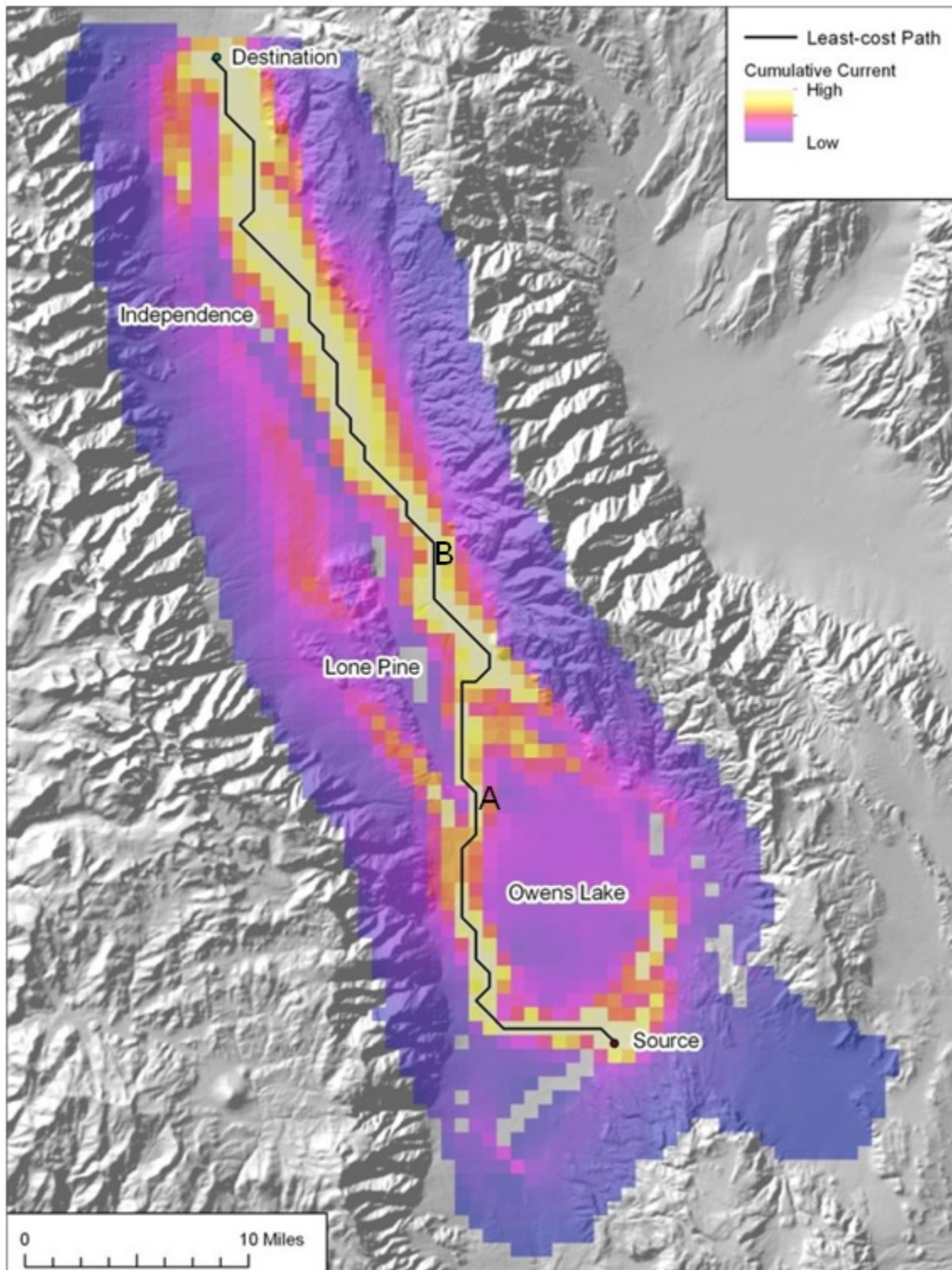
The colored area represents the movement corridor for range expansion. The letters A and B indicate pinch points.

The movement zone under current climate encompasses much of the area along Highway 395 north of Inyokern, and the China Lake Basin (Figure 47). In contrast, the movement zone using A2 2030 climate is restricted to the areas near Highway 395. The least-cost paths also differ depending upon the climate model that is used (Figure 47). Using the resistance map based upon current climate, three potential least-cost paths exist through the Ridgecrest/Inyokern area. One of these routes travels east of Ridgecrest, another west of Highway 395, and the third goes between Inyokern and Ridgecrest. In contrast, the least-cost path traverses around west of Ridgecrest/Inyokern. The reason for this change is that future climate is predicted to be too hot to be suitable for MGS at the lower elevations of the former path.

Figure 47: Least-cost path and cumulative resistance for Mohave ground squirrel connectivity between the central and northern populations.
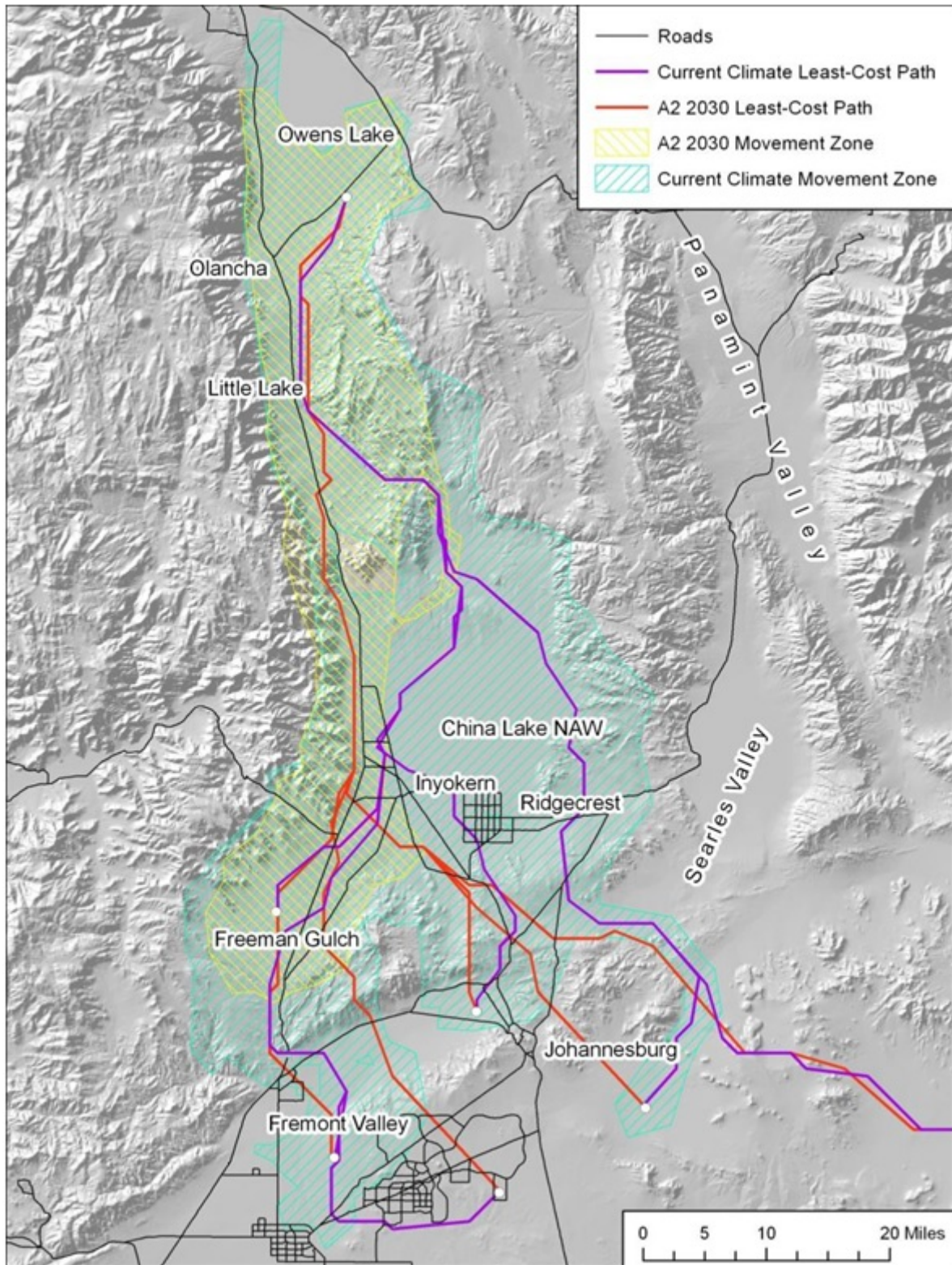
The cumulative current map (Figure 48) indicates that there may be many alternative dispersal paths allowing MGS to move north of the Ridgecrest/Inyokern area. Coso Basin appears to be an important area that might facilitate movement (A in Figure 48). North of Coso Basin one possible movement route goes into Cactus Flat (B in Figure 47) while another drops into Rose Valley (C on the map in Figure 48). A third less probable route travels parallel to Highway 395 (D in Figure 48). Pinch points exist near Ridgecrest and Inyokern (E in Figure 47), along Highway 395 (D in Figure 48), and between Coso Basin and Rose Valley (C in Figure 48). In contrast, the A2 2030 cumulative current map indicates fewer alternative routes, and the corridor along Highway 395 appears to improve with climate change. Based on the resistance map derived from A2 2030 climate, Coso Basin and Cactus Flat (A and B in Figure 49) continue to offer a suitable movement path even after China Lake Basin becomes less suitable. The cumulative current map greatly augments least-cost path analysis because it shows the location of potential alternative dispersal routes. The identification of pinch point areas is also valuable because such pinch points represent areas of high conservation priority given the caveats and assumptions underlying application of habitat models, landscape connectivity models, and downscaled climate change forecasts.

Figure 48: Cumulative current and least-cost path using present-day climate to model resistance as it relates to movement of Mohave ground squirrel.
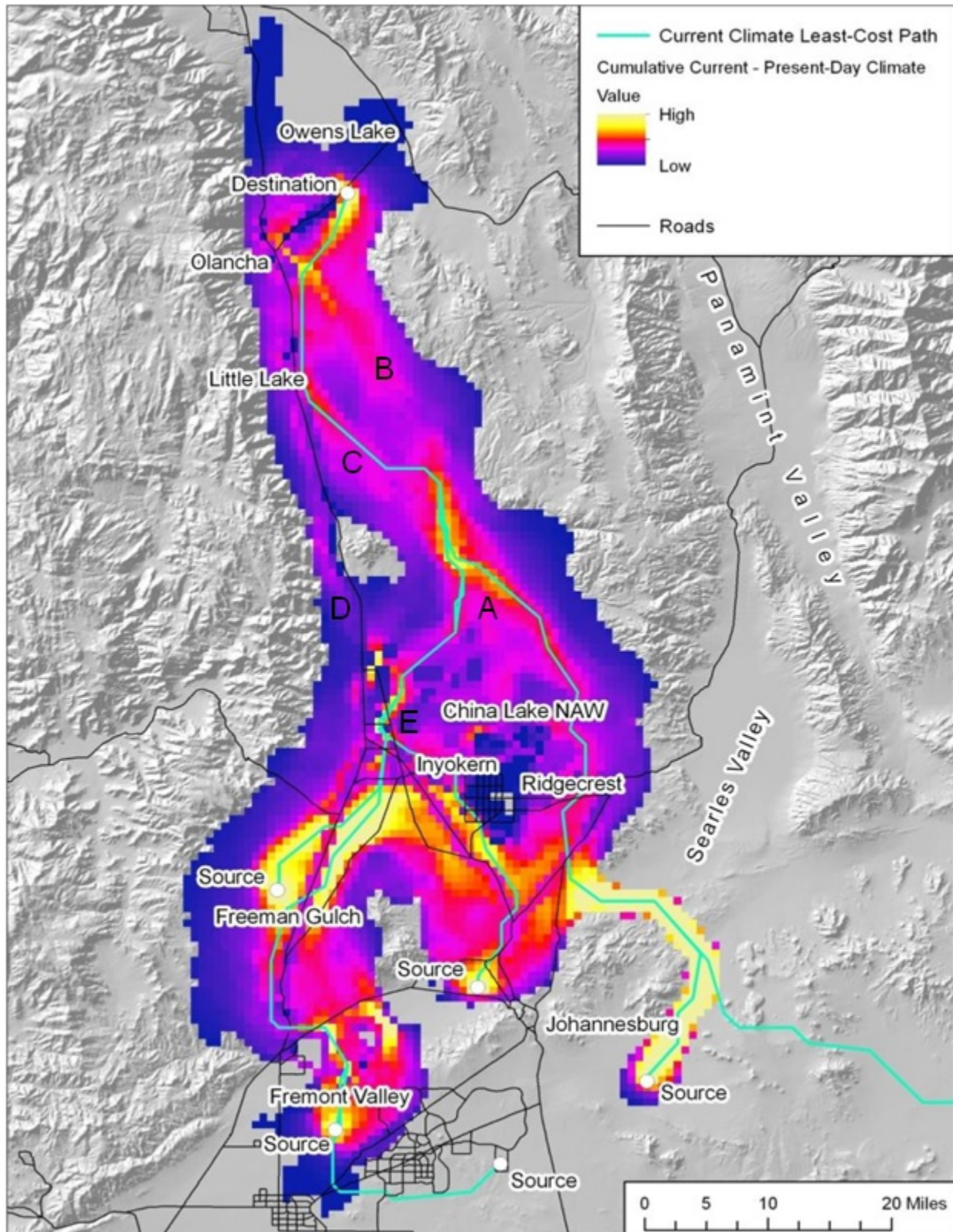
Figure 49: Cumulative current and least-cost path using 2030 climate with the A2 emissions scenario to model resistance as it relates to movement of Mohave ground squirrel.
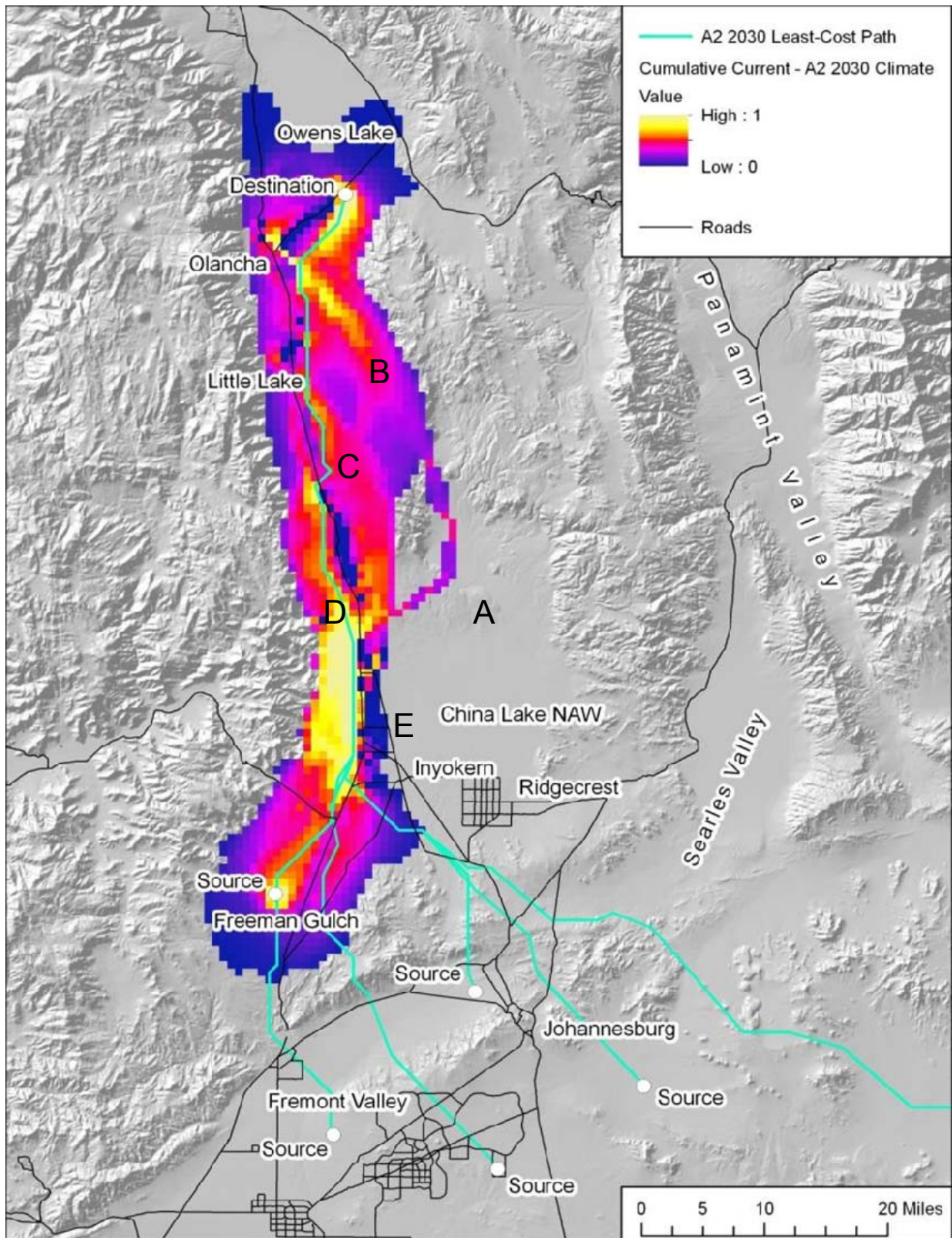
5.3.5 Effects of renewable energy development

Effects of renewable energy development, including solar, wind, and transmission corridors, decrease habitat by 2.3 percent assuming current climate, 3.6 percent in 2030 using the A2 scenario, and 3.6 percent in 2080 using the A2 scenario (Table 15). Although the overall loss of habitat is <5 percent, much of the lost habitat lies within core areas as defined in the West Mojave Plan (BLM 2005) and will most likely have a large effect on the central genetic cluster defined by Bell and Matocq (2011). The loss of connectivity was expressed as a difference in EC_{PC} of 7.2 percent assuming current climate, 3.9 percent in 2030 using the A2 scenario, and 6.9 percent in 2080 using the A2 scenario (Tables 14 and 15).

Table 15: Graph metrics for renewable energy development scenarios with A2 climate change scenarios and moderate land-use impacts estimation.

	Current – land use + development	A2 2030	A2 2080
Total Graph Length	17,714.00	9,269.16	5,018.44
Length of Largest Component	16,996.00	5,555.03	2,073.94
Proportion of Largest Component	0.96	0.60	0.41
Habitat Area	9,534.09	5,233.92	3,245.05
PC numerator	914,171.8	137,086.50	53,163.65
EC_{PC} index	956.12	370.25	230.57

To determine whether renewable energy development might fracture the habitat graph into multiple smaller components the total length of all links in the largest component were calculated and compared with the total length of all links in the graph. The length of the links in the longest graph component changes only slightly with 1.4 percent change for current climate, 3.5 percent change in 2030, and 7.1 percent change by 2080. Large decreases in the EC_{PC} index but small changes in the length of the largest graph component reflect the model assumption that wind energy development decreases habitat availability by 50 percent, which implies that the landscape is still somewhat permeable and movement can occur. In contrast, solar facilities are assumed to decrease the habitat availability by 100 percent. Locally some important links, such as the link connecting Freeman Gulch to Fremont Valley become severed resulting in severe losses in connectivity (Figure 50). Given the major changes in future distribution of suitable habitat predicted to result from climate change processes (Figure 41), loss of even a small number of links in the overall habitat graph might have important consequences for long-term population viability.

Figure 50: Change in graph structure (node and connection strength) due to proposed wind energy developments.
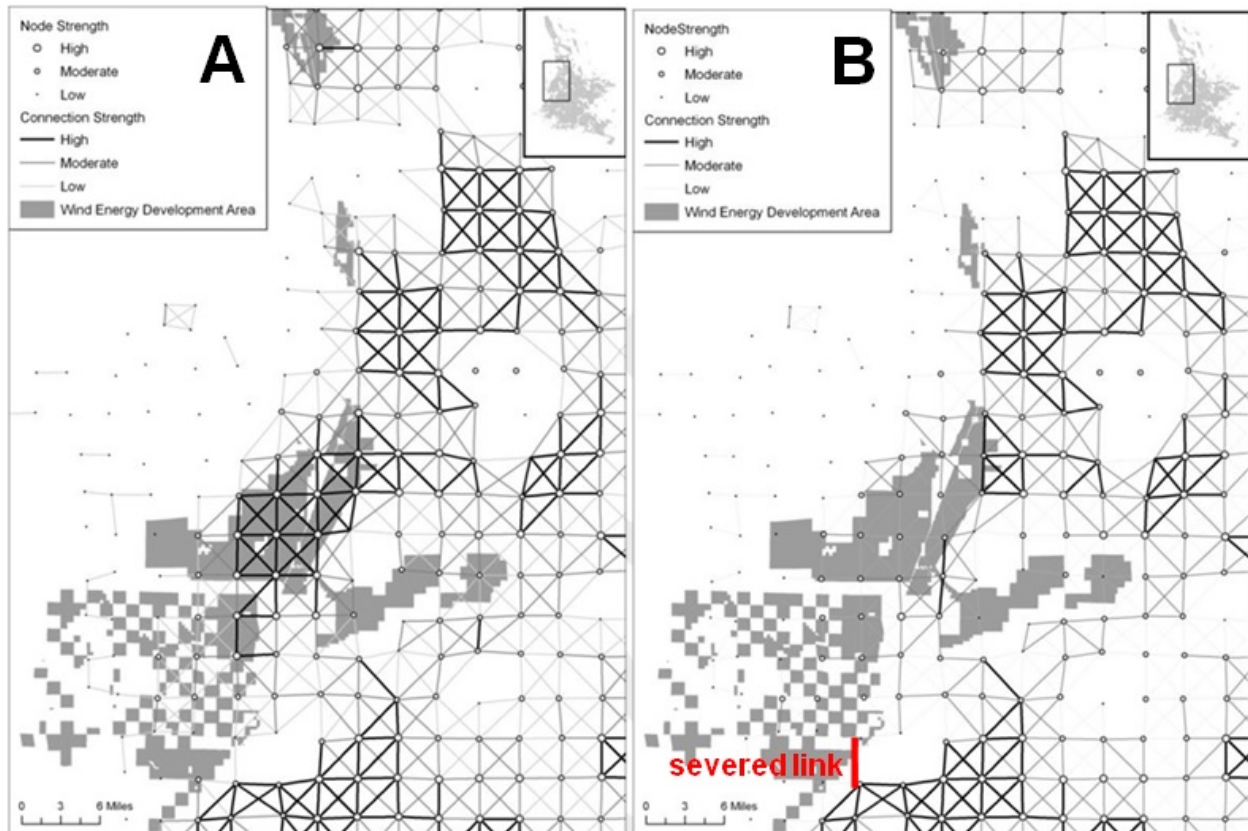
A) Graph structure prior to wind energy development and B) graph structure after wind energy development assuming that 50% of available habitat is lost and that resistance to movement is increased. In areas with wind energy development, node, and connection strength are generally decreased yet the presence of links remains intact. There are several important exceptions where key connections are completely removed, including the link that connects Fremont Valley to Freeman Gulch.

5.4 Study caveats and limitations

5.4.1 Uncertainty associated with using the habitat model as resistance to movement

Landscape resistance was represented by the inverse of the habitat occurrence model. This approach assumes that resistance to movement is negatively correlated with the probability of occurrence. Some authors have found that habitat quality may serve as a poor predictor of movement (reviewed in Spear *et al*. 2010). This is more likely to be the case for highly mobile species. However, the dispersal distance of MGS is short relative to the cell size used for modeling. Typical adult MGS home ranges cover < 2 ha. In contrast, natal dispersal by juvenile MGS occurs over mean distances of 1.5 km (Harris and Leitner 2005). Comparing these distances, MGS may be less capable of traversing unsuitable areas compared to other highly mobile taxa, such as birds and insects that are able to fly over hostile terrain, or large migratory mammals that move between seasonal ranges.

5.4.2 Uncertainty in land-use effects on resistance

The estimates of land use effects on resistance were based on expert opinion, an approach that has been heavily utilized by others in landscape genetics studies (Spear *et al*. 2010). To date there have been no studies to quantify the effects of roads and land cover on MGS movement, perhaps because the rarity of this species precludes techniques such as experimental translocation on opposite sides of a highway. Due to the lack of reliable quantitative data, the three estimates of land-use impacts on MGS movement were designed to bracket the range of values that could reasonably be expected. In addition to the three land use impact estimates, the one estimate that does not consider the impacts of land use apart from urban development was included. The moderate land-use impacts were used in combination with climate change scenarios and renewable energy development scenarios given that this represents the best estimate, while acknowledging that there is a significant amount of uncertainty surrounding land-use effects on resistance to MGS movement.

5.4.3 Uncertainty in climate change scenarios

There is significant uncertainty surrounding climate change scenarios. Climate change models differ based on both the GCM used as well as the emissions scenarios that are assumed (A2 versus B1 for example). Validation of climate change models is difficult because measurements cannot be made in the future that could be used to improve the models today. Thus, researchers are forced to assume that many of the conditions that prevail today will continue to be important going into the future. Another challenge with using GCMs is that these models are constructed at a spatial scale that is 1 degree or greater (11 km at this latitude), which is usually inappropriate for ecological modeling. Therefore, climate models must be downscaled to a scale relevant for ecological analysis (such as 1 km or less), which may involve a series of assumptions that introduce further error. Previously downscaled data (Flint and Flint 2012) were used and incorporated both the A2 and B1 emissions scenarios into analyses. Like the land-use impacts estimation, the use of both the A2 and B1 emissions scenarios were used to bracket the range of likely outcomes.

5.4.4 Spatial resolution and functional connectivity

Admittedly, there may be habitat variables that vary at spatial scales much finer than the scale used in this analysis and MGS habitat and corridor use may be strongly influenced by variables that are difficult to measure remotely (such as the fine-scale pattern of desert shrubs). The spatial resolution of the analysis, dictated by the habitat modeling effort (Chapter 2), may have limitations in describing patterns of "functional connectivity" (Stevens *et al*. 2006) for MGS. The spatial analysis of genetic structure reported in Chapter 4 strongly suggests that genetic structure varies at a finer resolution than the scale of landscape connectivity analysis (25 km^2) used here. Corridors as defined for MGS in this study do not refer to a typical dispersal movement within the lifetime of an individual ground squirrel, but rather, to more long-term, multi-generational species distributional shifts such as have likely occurred in the past, and need to occur for future response to global change.

The coarse spatial scales of the habitat model and connectivity analysis provide the opportunity for MGS to persist in future-climate scenarios even without long-range movement, through utilization of microrefugia (small areas of suitable habitat that are smaller than the 1 km^2 cell size used for habitat suitability models). Microrefugia are sites of locally favorable climate where species can persist despite climate trends that are regionally unfavorable (Dobrowski 2011). It is possible that MGS will be able to persist even in portions of the range predicted to become poor habitat, or that microrefugia can act as stepping stones that allow MGS distributional shift in response to changing climate over longer time periods than would otherwise be expected.

5.5   Synthesis and management limitations

Particular corridors and pinch points of critical importance to landscape connectivity of MGS were identified, both under current-climate and future-climate scenarios (Figures 46-50). Such locations should be protected from development where feasible, but should be re-evaluated as development scenarios change and climate change effects unfold. However, the modeled corridors are only of value where suitable habitat remains on either end to provide a source of dispersing individuals. It is important to conserve core areas of high-quality habitat, as well as the pathways for individual dispersal, and gene flow that provide critical connections among the high-quality habitat areas.

These results highlight the importance of conserving landscape connectivity through north-south trending, low-elevation valleys. Such valleys can function as important corridors for many desert species in facilitating latitudinal migration in response to climate change. Low-elevation valleys are expected to be of particular importance to fossorial rodents such as MGS for which soil texture is a critical component of habitat (Best 1995). Such species may be incapable of shifting their distribution upwards in elevation to reach suitable climates in a warmer world, given that soils of mountain slopes are generally thinner and of coarser texture than soils in valley bottoms and toe slopes.

The energy development scenario that was modeled was not a particularly extreme case, given that it was limited to projects already permitted for development. Although implementation of this scenario would only reduce most measures of landscape connectivity by 2 percent or less, local impacts could be severe and the reduction of habitat quality in areas of core habitat can be expected to negatively affect MGS populations. In addition, the importance of the developed area to landscape connectivity is predicted to increase by at least three-fold, given the climate change scenarios considered. It is thus critically important to consider future land-use and climate change when evaluating the outcome of any planned development for the requirements of biodiversity.

CHAPTER 6:
Summary, Synthesis, and Significance

6.1 Current Habitat

The initial habitat suitability model estimates pre-European suitable habitat of the Mohave ground squirrel (MGS, *Xerospermophilus mohavensis*) covering 19,023 km². Impact scenarios predicted that between 10 percent and 16 percent of suitable habitat has been lost to historical human disturbances, and up to an additional 10 percent may be affected by renewable energy development in the near future. These figures are the result of analyses conducted solely on public lands. State and private lands in the region also have pending proposals for renewable energy on 260 km², and an additional 3,500 km² may be available for renewable energy. The sum of potential habitat disturbance on public, State, and private lands could equal up to a quarter of historic suitable habitat from pre-European settlement levels.

While the analyses conducted here consider direct impacts from the footprint of renewable energy and associated transmission corridors, there are many indirect sources of environmental disturbance related to renewable energy development (Lovich and Ennen 2011). Some of those potentially important to the MGS include: increased fugitive dust and the release of chemicals such as dust suppressants, insulating fluids, and herbicides throughout the operational life of facilities, auditory interference from the sound and vibrations of turbines, increases in predators and invasive species that further alter system processes, and changes in surface flow of water that also influence vegetation that is important in these habitats. However, there is little research in the broader context of these topics for the Mojave Desert ecosystem, and less, if any, about the MGS.

6.2 Response to Climate Change

Modeling results predict future climate change projections will result in a loss ~52 percent to 84 percent of current MGS habitat for the different climate scenarios (GDFL A2 and GDFL B1) in the two time intervals analyzed (2030 and 2080). The same climate scenarios also predict habitat expansion of 37 percent to ~49 percent expanding mostly northward and eastward from current habitat. However, due to dispersal limitations, the amount of suitable habitat is predicted to show a net decrease in relation to future climate change. Successful MGS colonization of new habitat areas is required to contribute to population viability. Such colonization depends on accessibility (through habitat connectivity) to newly available areas. If limitations to dispersal are considered, then only ~71 to 74 percent of newly available areas would be available for MGS in 2030 (Chapter 3). It is important to note that some relatively extensive but disjunct areas of newly suitable habitat (e.g., near Pahrump, NV see Chapter 3) were identified by future habitat predictions but are not accessible to MGS, due to the many kilometers of inhospitable habitat (e.g., Death Valley and the surrounding terrain) that separate these areas from current habitat. Furthermore, the suitability of some of those areas appears to be transient through time and thus may be habitable in 2030, but uninhabitable by 2080.

Predictions of how organisms will respond to climate change tend to be somewhat pessimistic partly because the myriad of interactions occurring among species cannot be quantitatively addressed within the current habitat suitability framework. How MGS will respond to direct and indirect influences of future climate changes are perhaps the most speculative aspects of the analyses presented here. Although a great deal of current scientific expertise is devoted to understanding biological responses to climate change, the science is still young (Rodda et al. 2011) and the tools available to predict how organisms will respond to climate change are expected to improve.

Mohave ground squirrels depend on a variety of plant and also fungi and insect species to satisfy dietary requirements. The condition and phenology of plants depend on weather conditions and environmental conditions among years (Recht 1977). Yet, future plant community composition will vary with changing climatic conditions, and will be difficult to quantify for Mojave Desert species. Despite these challenges, there is enough information for some plant species to consider the future range changes for MGS and their food species. Two shrub species, winter fat (*Krascheninnikovia lanata)* and spiny hopsage (*Grayia spinosa*) are considered important as MGS food items. Interestingly, MGS co-occur in the extreme southwest distributions of the two shrubs (Benson and Darrow 1981) and these shrubs' current distributions overlap the entire future range of MGS as illustrated in Chapter 3. Similar to MGS, it is unknown how the shrubs will respond to fluctuating climate conditions, but at least the challenge of dispersal in order to match future climate shifts is not a challenge for these species. By searching the fossil record and comparing it to paleoclimate data, researchers learned that many plant species have already survived conditions comparable to future predictions (i.e., temperature increase of 4 °C over 60 years) and in some cases actually expanded their ranges (Willis *et al.* 2010). Thus, paleohistory indicates examples of less than dire consequences of comparable climate change, yet our best and most contemporary tools now indicate that MGS likely faces habitat losses with climate change.

6.3   Landscape Genetics

Landscape genetics can identify historical and ongoing genetic variation and is used here to highlight areas that may serve as important pathways facilitating gene flow among populations and allowing movement in response to climate change. Based on analyses in this report, some populations may experience dramatic declines in site occupancy and genetic diversity in response to climate change and landscape disturbances. The opportunity to couple genetic analyses with the newly available information reported in earlier chapters of this report, provides an unprecedented opportunity to gain insights into genetic variation in MGS within the context of habitat suitability and connectivity.

The three genetic groups found in the northern, central, and southern portions of the range, have relatively low levels of population differentiation indicating that gene flow has been generally high among MGS. This is especially true in the southern part of the range and is thought to be due to relatively large contiguous areas of suitable habitat, where multiple potential routes for genetic exchange may lead to more genetic exchange over time. The strongest factor contributing to genetic differentiation among the populations is related to the

episodic flooding of lakes and rivers of the Owens River system that resulted in isolation of different groups throughout the Holocene. These areas are at low elevations and may continue to provide filters among populations to this day. This pattern could be better understood with additional genetic sampling in the area of China Lake. Although landscape genetics patterns can be differentiated at this time the pattern could be enhanced by additional sampling at scales finer scales across the landscape. Fine scale genetic analyses coupled with direct measurements of dispersal distances indicate that average effective dispersal of MGS may occur at > 1 km. This is important because most of the modeling in this MGS research project was conducted at a 1 km scale, thus the scale of the models is compatible with the actual dispersal distances of the focal species. The practicality of this comes with understanding that squirrels can hypothetically access habitat from one cell in a model to another. Furthermore, this information can be used to guide future research endeavors to understand source/sink dynamics with respect to habitat quality, and to identify the types of features that may restrict or enhance gene flow.

Simulations of MGS genetic response compound the outcome of future climate scenario predictions, potentially resulting in dramatic losses of genetic variation and local fixation throughout the range, possibly leading to population collapse. Like habitat modeling, landscape genetics is a new science and these results should be considered conservatively (Landguth and Cushman 2010). The potential consequences of landscape genetics in relation to climate change alone, must be carefully considered, and conservation plans that encompass the interaction of climate change with land development from renewable energy should be developed cautiously and conservatively.

6.4   Landscape Connectivity

Landscape connectivity provides a robust procedure for habitat prioritization based on the importance of habitat units supporting habitat connectivity. Connectivity is crucial in that metapopulations are maintained in the face of disturbances that result in local extirpations. Connectivity is the means by which populations (and ultimately species) respond to changes in the distribution of habitat through time and space. The landscape connectivity analyses described here provide syntheses of far ranging topics by identifying: important habitat patches for MGS and other important community members; how animals may function within and among those patches; important gene flow for viable populations; and dispersal and movement in response to a climate change, development projects, and renewable energy projects in particular. While genetic analyses indicated relatively well-connected genetic units across the MGS distribution, connectivity analyses identify 14 particular areas that are disproportionately important for connectivity among suitable habitat patches (Figures 37a an 37b). Among these areas, some appear to be critically important because they provide essential landscape connectivity among patches that are central to MGS populations, with few or no alternatives should those connections be severed. Others areas are critically important to MGS conservation because they provide connectivity among patches that are peripheral to population centers, yet provide routes by which MGS may respond to shifting habitat areas in response to climate change. Furthermore, a comparison using these methods with other species indicates that MGS conservation plans may indeed benefit from connectivity analyses. Further analyses identified

areas on the landscape known as bottlenecks or pinch points that may be essential areas for connectivity. One such area is in the Coso Basin (area 'J' on Figure 38) that is identified as a gateway between current northern and more southerly populations. Development appears to have a disproportionately large negative impact on MGS habitat possibly due to the diffuse road networks and other associated disturbances. Based on several methods used here, general habitat connectivity for MGS is relatively intact at this time (especially in more southerly areas); however some important areas show diminished connectivity including areas near Palmdale, between the Fremont Valley and Freeman Gulch, and also near Ridgecrest.

Future climates are predicted to reduce the overall area of habitat available to MGS and to reduce connectivity of current habitat patches to a much greater extent than land-use impacts. While the current movement corridors described here provide multiple alternative routes in the greater Ridgecrest area, predictions for corridor locations in future scenarios are more restricted. North of Inyokern MGS movement alternatives are reduced to a single broad corridor along Highway 395, with one possible exception (Figure 46). In the future, MGS range shifts may be facilitated by future habitat corridors directly through the Owens Valley. The east side of Owens Lake, with more contiguous habitat available, is predicted to be more preferable that the west side.

The energy development scenario the authors modeled was not a particularly extreme case, given that it was limited to projects already permitted for development. Planned renewable energy developments (wind, solar, and transmission corridors) are generally predicted to reduce available habitat by < 5 percent, which is small compared to other development. The assumption that wind energy developments are 50 percent more permeable to MGS than solar energy developments had a large influence on their relative impacts to MGS. In fact, these were expert opinion approximations and more research on the use of habitat by MGS would inform this discussion considerably. Those predicted losses are disproportionately important because the proposed developments exist in core habitat areas of high habitat suitability. The importance of these losses may be compounded by habitats lost due to future climate changes.

6.5   Synthesis

This research project required the compilation of all available MGS locality data including recently acquired unpublished data sets, which were reviewed for accuracy and quality assurance. The data were then organized, and the result is the most comprehensive MGS data set available today. This project used state-of-the–art analyses for habitat suitability, future habitat predictions, landscape genetics, and habitat connectivity using novel approaches. The custom data sets that were specifically developed are now available for other research projects as well. Some of the data layers generated in this study are posted for public use on the Conservation Biology Institute's Data Basin Website (http://databasin.org/), and should be useful for future research endeavors, as well as to agencies and developers in siting renewable energy projects and conservation planning, impact analyses, and mitigation. Data on MGS habitat suitability from this project is being used to develop conservation and renewable energy alternatives exist for the Desert Renewable Energy Conservation Plan and to assess impacts.

Habitat suitability modeling can be a useful conservation management tool (Graham *et al.* 2004, Elith and Leathwick 2009a). Due to the highly technical quantitative elements, rapid development of new techniques, and widespread use of these recently developed tools, the caveats provided by authors of such work should be heeded carefully. Each chapter in this report provides detailed cautionary instructions for the reader. While the tools used to project current and future habitat models are state-of-the-art and as indicated such tools continue to develop and improve at a very rapid pace. Changes in land use also continue to change at a very rapid pace. Thus our predictions about the juxtaposition and potential influence of development activities across the landscape may be the best available knowledge – at the moment – but these projects are spatially static in the analyses and cannot realistically account for the changes in energy technology and human population distributions that will obviously affect MGSs, their habitats, and the entire desert landscape. These admonitions are provided in part to ensure that the information is used with the proper caution to inform management and policy decisions without adding to controversy. Controversies over conservation management policy have arisen over the data, methods, and interpretations of other habitat suitability modeling from past projects (see Rodda et al. 2008, Pyron et al. 2008 and Rodda et al. 2011). While such debates can be interesting for participants and a necessary part of the scientific process, they can also temporarily obfuscate fact and deter resolution of societal issues.

Mohave ground squirrel habitat losses appear imminent relative to climate change, general expansion of human activities, and energy development in particular. However the degree of change imposed by the factors that can be controlled (i.e., human-related development) within the MGS habitat are subject to enacted conservation management plans. Guidelines provided in consideration of the costs and benefits of assisted migration suggest that planning for such management activities should not be delayed (McLachlan et al. 2007). Some of the direst predictions about losses to habitat, habitat connectivity, and genetic diversity depend on the assumptions of future climate scenarios and the concern for the future of many species is widespread (McLaughlin et al. 2002). Although a great deal of current scientific writings conclude imminent losses of biodiversity, some recent works have provided examples from the paleo-record of species indicating that species and at least portions of communities apparently survived previous climatic episodes that were comparable to those predicted in our future (Willis et al. 2010), but it should be noted that species reactions to these previous climate change events were unhindered by fragmentation of habitat by human development.

GLOSSARY

Term	Definition
AICc	Akaike information criterion
AUC	Area Under the receiver operating characteristic Curve
BI	Boyce Index
BLM	Bureau of Land Management
CEHCP	California Essential Habitat Connectivity Project
CNDDB	California Natural Diversity Data Base
CI	Confidence interval
DEM	digital elevation model
DNA	Deoxyribonucleic acid
DRECP	Desert Renewable Energy Conservation Plan
DTNA	Desert Tortoise Natural Area
EC$_{PC}$	equivalent connected area index
ESRI	Environmental Systems Research Institute
FWS	Fish and Wildlife Service
GAIN	improvement in penalized average log likelihood over null model
GHG	greenhouse gas
GIS	Geographic information system
GFDL	Geo-physical Fluid Dynamics Laboratory
GCM	Global climate model
IPCC	Intergovernmental Panel on Climate Change
MaxEnt	Maximum Entropy model
MODIS	Moderate Resolution Imaging Spectroradiometer
MGS	Mohave ground squirrel
MRLCC	Multi-Resolution Land Characteristics Consortium
NLCD	National Land Cover Database

Term	Definition
NOAA	National Oceanic Atmospheric Administration
NREL	National Renewable Energy Laboratory
OHV	Off-highway vehicle
PC	Probability of connection index
PEIS	Programmatic Environmental Impact Statement
SDM	Species distribution model
TIGER	Topologically Integrated Geographic Encoding and Referencing
UNICOR	UNIversal CORridor network simulator
USGS	United State Geological Survey
USRED	Utility scale renewable energy development

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